ILLINOIS BIOLOGICAL MONOGRAPHS

VOL. XV

No. 3

PUBLISHED BY THE UNIVERSITY OF ILLINOIS
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
URBANA, ILLINOIS
1937

1000—8-37—12024

UNIVERSITY
OF ILLINOIS
PRESS

STUDIES ON THE BIOLOGY OF THE CRAYFISH CAMBARUS PROPINQUUS GIRARD

WITH 46 GRAPHS

BY

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Contribution from the Zoological Laboratory of the
University of Illinois
No. 509

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ACKNOWLEDGMENT

The writer wishes to express appreciation to Dr. H. J. Van Cleave for suggesting the subject of these studies and for cooperation and aid during the progress of the work. Thanks are due also to Dr. John D. Mizelle, Mr. Philip F. Van Cleave, and Mr. W. C. Starrett, for their assistance in the making of collections.

Mrs. Hugh R. Smith, of Akron, Ohio, kindly consented to allow the writer to refer to her unpublished research material on *Cambarus propinquus,* most of which was compiled during 1910 and 1911 in the same general area in which the writer's research was conducted.

The main portion of the bibliographic work in connection with this study was carried on in the library of the University of Rochester while the writer was serving as field biologist for the Monroe County Park Commission, at Rochester, New York. The cooperation of the officials of the library, and of Mr. F. T. Burke, Executive Secretary of the Commission, made possible the completion of the work.

INTRODUCTION

In spite of the fact that the crayfishes are widely used for laboratory studies, very little work has been done on the developmental cycles of individual species in particular areas. Studies of seasonal changes have been almost wholly neglected. The available information concerning maximum size and length of life is of the most fragmentary sort and has in most cases been based upon observations of animals in aquaria and under unnatural conditions.

This lack of specific and detailed information is not peculiar to the crayfishes. Van Cleave (1932) has pointed out that the life cycles of very few species of animals have been carefully studied. Some forms possessing economic importance and forms causing disease have received attention, but others which are equally conspicuous have been relatively neglected so far as life history studies are concerned.

In many cases a more or less heterogeneous collection of material has been lumped together as knowledge of the life cycle of "the earthworm" or "the crayfish" and has been accepted as such in the absence of more complete studies. As was further shown by Van Cleave (1932) the general acceptance of such studies may be traced in part to an assumption that species which are closely related taxonomically have identical life histories. Such an assumption is unwarranted since careful investigation of any group of related species shows that the life histories of individual species of the group may differ markedly from one another in details. The most that can be expected in studying related species is the occurrence of parallelism in the main points of their life cycles.

The group of the American crayfishes first attracted the attention of zoologists near the middle of the nineteenth century. Girard, in 1852, published a short article in the Proceedings of the Philadelphia Academy of Natural Sciences under the title of "A Revision of North American Astaci with Observations on Their Habits and Geographical Distribution." In this article he named a number of new species, of which he gave brief and very inadequate descriptions. Hagen (1870) published a "Monograph of American Astacidae," which was very comprehensive, and which makes mention for the first time of the sexual "forms" of the male in the genus Cambarus. This phenomenon was further elaborated upon by Faxon (1884) who first gave the true explanation of its occurrence. Faxon (1885) published a "Revision of the Astacidae," bringing together existing information regarding species and localities. This work also contains observations on the young of three species of crayfish *C. clarkii, C. gracilis,* and *C. bartonii.* Andrews (1895) described in detail the process of conjugation and egg laying in *C. affinis.* In 1902, Steele published detailed observations on the young of *C. virilis.* Ortmann (1905)

revised the classification of the genus Cambarus by creating within it six subgenera, and in 1906 he published a very good life history of *C. obscurus*. Andrews (1907) published a comprehensive description of the appearance and growth of the young of *C. affinis*. This contribution was based, however, entirely on observations made in the laboratory.

Andrews' work embodies the chief observations on crayfish life history which have been incorporated in the textbooks of zoology in this country. All too often the student is led to think that the observations of Andrews on a single species are valid in detail for all species of the genus Cambarus.

In the present study a detailed and extended investigation has been made of the life cycle of a particular species of crayfish in a closely circumscribed locality. The particular species selected for the present study was *Cambarus propinquus* Girard. This is the most common of the crayfishes on the eastern side of the Ohio-Mississippi watershed in Illinois. It is found abundantly in small streams of the area, and is available for observation and collection at all seasons of the year.

METHODS

The methods used throughout the course of this work were observational and statistical. The intention was to lay emphasis on the study of the animals in their natural habitat and under natural conditions, with the hope of thus obtaining more accurate and significant data than those obtainable by studying the animals under laboratory conditions.

When the animal is removed from its natural environment and taken into the laboratory, the conditions under which it is placed are at best but a poor imitation of those which it normally encounters. Such innumerable, intricate environmental relations exist in nature that it would be hardly possible for an experimenter to duplicate them in a laboratory, even if the workings and interrelations of all environmental factors were understood. The reactions of an animal throughout the course of its life history come about as a result of the totality of all environmental relations plus the internal factors inherent in the animal itself. Therefore, any laboratory study of a life history problem, at least of the life history of a relatively large, free-moving species, is, in the writer's opinion, open to question. For this reason, in the carrying out of this work, it seemed best to rely on intensive field study.

According to the original plan of investigation, it was intended that collecting and observational trips should be made to the area under study at intervals of exactly two weeks. Circumstances, however, interfered with the fulfillment of this schedule. Periods of high water sometimes made collecting impossible, and numerous other factors precluded ad-

herence to an absolute schedule. However, at some particularly significant periods, as during the egg-carrying season in the spring, it was sometimes possible to make weekly collections and observations.

When collections were taken, field notes were made regarding environmental conditions and the relations of the crayfishes to their habitat. Particular attention was paid to their position with regard to the stationary features of the environment, and the degree and kind of activity in which they were engaged.

Collections were made by either of two methods. During the summer and early fall the animals could be taken with a dip net. This method was especially useful during early summer when the season's young were small, although adult individuals were obtained at the same time. During the late fall, winter, and early spring it was found more satisfactory in most cases to use a minnow seine. By the use of the seine a larger area of stream bottom could be covered, and the sampling over the area could be done more thoroughly. A variation of the first-mentioned method was the "still-hunt." This was used occasionally on sunny days in the winter when the water was exceptionally clear. At such times the crayfishes could easily be seen sitting on the bottom, or partially concealed under stones, and could be picked up one at a time, either with a dip net or by hand.

From the beginning of the present study the desirability of obtaining information regarding particular individuals was realized, but limiting factors seemed to preclude this under conditions of nature. The important part played by ecdysis in the physiology of the animals and particularly in the growth processes eliminated the possibility of attaching tags of any sort to the body, and likewise ruled out the possibility of applying any mark for later recognition on the shell by means of paint or pigment. Furthermore, the powers of regeneration are so marked in crayfishes and accidental injury is of such frequent occurrence that removal of appendages or parts of appendages is of no value for later recognition of individuals. This method was attempted during the second year of the study, but without success. Therefore, all of the previously utilized methods of marking individuals for recapture and study were impracticable for use in this study of crayfishes.

In consequence of this the collections which were taken were treated statistically. The living animals of each collection were separated according to sex. The males were further studied and notes were taken for each individual as to the "form" of the copulatory appendages. Seasonal limitations of occurrence of the "first form," "second form," and juvenile males were thus established for the habitat under consideration.

It seemed desirable to obtain a single measurement on each individual which would serve as an index to its size and general development, and

also one which could be used equally well for both sexes. The works of Huxley (1924), Shaw (1928), Bush (1930), Bush and Huxley (1930), and others in connection with heterogonic growth of different body parts in the group of Crustacea show that the growth rates of different body parts bear relations to one another which are definite and mathematically expressible. Thus the relation of the rate of growth of the chela of the male to the rate of growth of the body as a whole can be expressed as a constant, the chela increasing in absolute size more rapidly than the body, though at a constant rate. Such relations, however, are chiefly discernible in connection with secondary sexual characters, and differ radically in the two sexes. With grosser body measurements in which the two sexes do not differ the relations are relatively constant throughout life, and may be used as indices of individual and group development.

Therefore, it was necessary to choose a body measurement of relatively gross nature, and one in which the sexes showed no apparent difference in regard to relative size or form. In addition it was necessary to choose a measurement which could be taken in the field with a minimum of time and effort, and one which would not be affected by the movements of the animal during the process of measurement. The length of the cephalothorax from the tip of the rostrum to the anterior end of the abdomen was chosen as the measurement which best fitted all requirements. Furthermore, this measurement could be easily translated into terms of approximate body length, since it represents 49% of the total body length in all periods of the life history after the young become free-swimming. For purposes of general comparison with published data in which the only measurement given was the total body length, the writer has found it practicable to consider the cephalothorax length as one-half of the total body length.

The length of the cephalothorax was used by Smith (1910-11) in her unpublished studies of *C. propinquus* at Urbana, Illinois, and more recently by Creaser (1933 and 1934) in his studies of the same species in Michigan.

In the present study the measurements were taken in the field, and as soon as the necessary observations were completed the animals were returned to the water. The individuals were measured by means of vernier calipers, and the measurements were recorded to the nearest tenth of a millimeter. In conformity with the general intention to preserve as nearly natural conditions as possible, the animals were handled only twice during the entire operation and were held out of the stream for as short a period as possible.

The measurements of the population sample examined on each collecting trip were plotted graphically, using one millimeter as the unit of construction. In reducing the fractional measurements to one milli-

meter size classes, those from 9.6 to 10.5 were counted as 10, those from 10.6 to 11.5 as 11, etc. In constructing the graphs it was found most satisfactory to let the abscissas represent cephalothorax lengths, and the ordinates represent numbers of individuals. This seemed to result in the separation of the population into natural size groups. The modes of these size groups were then plotted on a composite graph (see Graph 3) in which the ordinate was made to represent the position of the modes in millimeters, while the abscissa was made to represent time in weeks. By connecting the points denoting the same size groups in different collections, these size groups came to be represented by lines. They could then be followed in their growth and development through the season and could be related to molting and other life history phenomena.

In the study of each population sample, separate plottings were made for the cephalothoracic measurements of the members of the two sexes. These plottings were made by the same method which was used for plotting the measurements of the general population, and the distribution curves for the males and females in each collection were placed on the same sheet as the distribution curve for the general population taken in the collection. This placed the curves in a position convenient for purposes of comparison.

A detailed account of the development of statistical methods of life history study is given by Van Cleave (1931). The particular method used in the present study is an adaption of the method used by Van Cleave and Markus (1929) in the study of the blunt-nosed minnow, *Hyborhynchus notatus;* by Foster (1932) in the study of the fingernail shell, *Sphaerium solidulum;* and by Van Cleave and Lederer (1932) in their study of the snail, *Viviparus contectoides.* Similar methods were used by Creaser (1933 and 1934) in his study of *C. propinquus* in Michigan.

DISTRIBUTION OF THE SPECIES

The specimens of *C. propinquus* which Girard first described came from Lake Ontario and western New York. The species is now known to occur also in Pennsylvania, Ontario, Quebec, Ohio, West Virginia, Indiana, Michigan, Illinois, Wisconsin, Iowa, Minnesota, and Nebraska. It is found chiefly and most abundantly in the Great Lakes drainage (Ortmann, 1905 and 1906; Graenicher, 1913; and Turner, 1926). However, it has migrated extensively into the Ohio and Mississippi River systems (Ortmann, 1905 and 1906) and even into the Missouri River system (Engle, 1926).

It is found in the Great Lakes drainage of New York and southern Canada (Ortmann, 1905); in the Great Lakes drainage of Pennsylvania and Ohio (Ortmann, 1906); and also in a restricted area of southern

Ohio (Turner, 1926). It occurs in the extreme northern tip of West Virginia (Newcombe, 1929). It is found throughout the states of Indiana and Michigan (Hay, 1896; Pearse, 1910). It is most abundant in the Great Lakes drainage of Wisconsin, but also occurs to some extent in the Mississippi drainage of that state (Graenicher, 1913). It occurs in the Mississippi drainage of Iowa and Minnesota (Ortmann, 1905), and colonies of it occur in the Big Blue River drainage of southeastern Nebraska, which is a part of the Missouri River system (Engle, 1926).

In Illinois the species is found in both the Mississippi and Ohio River drainage systems, and occurs in both the northern and southern sections of the state. Harris (1903) lists it as occurring in the Illinois River drainage in McLean, Tazewell, and Macon counties. The writer has in his possession a collection of *C. propinquus* taken by Mr. John Cralley in the fall of 1932 in the vicinity of Carmi, which lies within the Ohio River drainage of southern Illinois, showing that the species occurs in that section of the state also.

C. propinquus gives place in Ohio (to the south of the Great Lakes drainage) to *C. propinquus sanbornii,* and this in turn gives way in central and southern Pennsylvania to *C. obscurus.* These three forms constitute a very closely interrelated group. It is the belief of Ortmann (1905 and 1906) that these three types of crayfishes originated in the three principal tributaries of the Erigan River, a pre-glacial river which drained most of the present-day Ohio Valley and Great Lakes basin and emptied into the Gulf of St. Lawrence. With the temporary damming of the old river outlet during the glacial period and the formation of a new drainage outlet to the southwest (the present Ohio), the three types of crayfishes came to occupy the lower, middle, and upper portions of the Ohio River valley.

C. propinquus, being more strategically located in relation to the newly exposed territory from which the ice had receded, recolonized the Great Lakes basin, and migrated westward into the Mississippi and Missouri River drainage systems, while *C. propinquus sanbornii* and *C. obscurus* did not increase their range to any marked extent.

HABITAT

The principal collecting area consisted of a section of about 150 yards of a small stream in the north edge of Urbana, Illinois. This stream is known locally as the Saline Drainage Ditch. It rises in the northern part of Champaign County, Illinois, and flows into the Vermilion River. This in turn empties into the Wabash River and forms a part of the Ohio River system. Studies were carried on at this collecting station during two years, from June, 1932, to June, 1934.

At the place where the collections were taken the stream contains two small areas of rapids, but otherwise it is very slow flowing. In the rapids the bottom consists of numerous stones lying upon a substratum of coarse gravel. In other parts of the stream the bottom consists of a mixture of silt and sand, over which are scattered stones of various sizes. When the stream is at a normal level the depth in the collecting area varies from a few inches at some points along the edge to about three feet in the deepest places.

The shallow areas near the banks support a rank growth of semi-aquatic vegetation during the summer. Other vegetation consisting of weeds, sedges, and grasses grows on the banks at the edge of the water and overhangs into the water. The banks are either unshaded or only partially shaded by trees and shrubbery.

In the late fall the stream becomes nearly filled in places with drifts of water-soaked dead leaves. This is particularly true if there is a low water level during October and November. Such leaf drifts persist during most of the winter behind clusters of dead vegetation and in the bottoms of the deeper pools.

The stream was not ice bound for any considerable time during either of the winters while the study was being conducted (1932-33 and 1933-34). During each winter there were a few times when it was necessary to break the ice in order to secure collections, but even at such times the areas of rapids were open.

The stream is subject to considerable variation in amount of flow on account of the fact that it is dependent on surface run-off rather than on springs or other relatively constant sources of supply. During the spring seasons of 1933 and 1934 there were periods of high water during which the collection of crayfish in large quantities was difficult or impossible. Similarly, periods of prolonged dry weather caused a marked fall in the water level.

During the fall of 1932 supplementary studies were carried on at a collecting station on Stony Creek, a small stream in the western part of Vermilion County, Illinois, about 25 miles east of Urbana, Illinois. This stream also flows into the Salt Fork of the Vermilion River.

This stream is rock-bottomed, and in general is much more swift flowing than the Saline Drainage Ditch. It consists of extensive areas of rapids with deep pools between. However, it, likewise, is subject to wide fluctuations in amount of flow, depending on local rainfall.

The portion of the stream from which the collections were taken consists of two habitats, an area of rapids and a pool located at the foot of the rapids. The rapids measure from 6 to 12 inches in depth and the pool from 2 to 3 feet in depth when the stream is at a normal level. The

vegetation at the edge of the stream is relatively rank, and is of the same general character as that described for the Saline Drainage Ditch. Here, however, the banks are low, and in themselves offer little or no protection to aquatic organisms. The water is very clear, and carries very little sediment even in flood times.

RELATION TO ENVIRONMENT

The species of Cambarus may be classified into two major groups on the basis of their habitat preferences. These two groups are: (1) those species which spend a part or all of their time on lowlands in burrows which extend down to ground water; and (2) those species which are always found in open water, either small streams, rivers, or lakes. *C. propinquus* belongs to the second of these two classes.

Individuals of this species do not make burrows, even during periods of adversity, although occasionally they may make tunnel-like excavations in the banks of streams, slightly below water level (Hay, 1896; Harris, 1903; Engle, 1926). Therefore, except for the possibility of occasional overland migrations, they are confined to permanent bodies of water, and accomplish their entire life cycle within the stream, lake, or pond in which they are found. Within a particular body of water, however, they exhibit very definite relations to local variations of habitat, and these relations vary markedly at different seasons of the year, and at different periods of the life cycle.

During the summer months the young crayfish are found in the surface layer of water among the weedy vegetation which grows along the edge of the stream. They usually select the shallower areas where the vegetation is more abundant, but they are also found in the surface water over deeper areas, provided vegetation is present.

The adults select the bottom of the stream at all seasons, and are rarely taken near the surface. In the summer they are usually found under stones or other objects in the shallower places, either along the banks or in the shallower pools and rapids. Since the young crayfish are also found along the banks during the summer months, collections taken in summer along the shallow, weedy portions of the stream yield representative samples of all sizes and age groups. However, such collections are really taken from two distinct strata of crayfish population: (1) the bottom-dwelling adult population; and (2) the surface-dwelling juvenile population.

In late summer the young crayfish leave the surface layer of water and select the shallow areas of stream-bottom as do the older individuals. Therefore, there is no appreciable difference in habitat relations between the adults and the season's young during August and early September.

After the middle of September all of the crayfish show a definite tendency to leave the shallow areas and resort to the deeper pools. This tendency is most marked, however, among the large and mature individuals. Not only the class which has been adult during the summer but also those among the season's young which have just attained maturity show a more marked tendency to leave the shallow water than do the immature individuals. Thus a partial segregation of mature and immature individuals takes place.

TABLE 1.—DISTRIBUTION OF MATURE AND IMMATURE INDIVIDUALS IN SHALLOW AND DEEP WATER OF STONY CREEK*

Date of collection	Mature individuals			Immature individuals		
	Number collected	Percentage in deep water	Percentage in shallow water	Number collected	Percentage in deep water	Percentage in shallow water
Oct. 2, 1932	39	51.7	48.3	100	25.	75.
Oct. 13, 1932	30	80.	20.	100	41.	59.
Oct. 27, 1932	50	60.	40.	70	42.8	57.2
Nov. 10, 1932	33	60.7	39.3	84	44.	56.

*All collecting on Stony Creek had to be done with a dip net, since the bottom is too stony for a seine to be used successfully; and the dip net had to be used "blindly" in the deep water, while in the shallow water the individuals could be seen and dipped out to better advantage. Since there was a preponderance of mature individuals in the deep water, and a preponderance of immature individuals in the shallow water, this unequal sampling resulted in a preponderance of immature individuals in all collections taken during the fall.

Table 1 shows the distribution of mature and immature *C. propinquus* taken at Stony Creek during October and November, 1932 as related to shallow and deep water habitats. The size of 20 mm. cephalothorax length was taken as the approximate lower boundary of sexual maturity in both sexes.

It will be seen that in these collections the segregation was only a partial one, representing a difference in relative abundance of the two size classes in the two habitats, rather than a clear-cut segregation. However, in every collection the major portion of the mature population was taken in the deeper water, while the major portion of the immature population was taken in the shallower water.

This tendency towards segregation was also found among the crayfish population of the Saline Drainage Ditch. In a collection of 75 individuals taken from this stream on November 17, 1932, 63.3% of the mature group were found in the deep water, and 36.7% were found in the shallow; while of the immature group only 31.8% were found in the deep water, and 68.2% in the shallow.

With the beginning of winter this tendency towards segregation largely disappears. Most individuals of all size groups leave the shallow areas and conceal themselves in dead leaf drifts or under stones in the

deeper portions of the stream. Smith (1910-11) found as many as six individuals partially buried in the mud and detritus under one small stone in November. She found further that there was a tendency for them to seek the shelter of larger stones and to bury themselves more deeply in the mud, as the winter became more advanced.

The crayfish of this species show some activity all during the winter. However, in the winter the effects of environmental factors which regulate the time and amount of activity become more noticeable. Apparently one of the principal factors regulating the winter activity of *C. propinquus* is sunshine. There is some correlation between sunshine and amount of activity of this species at all seasons. Collections taken on sunshiny days, even during the summer, invariably yielded better results than did those taken on days when the sun was not shining. During the late fall and winter, however, the activity of the animals becomes even more closely correlated with sunshine.

After the middle of November, if the sun is shining, the crayfish show a limited amount of activity during the middle of the day, but none at all at any other time. This period of activity begins at about 11:00 A.M., and lasts until about 2:00 P.M. On cloudy days, or at times other than near mid-day when the sun is shining, the animals remain concealed.

During the late fall and winter, therefore, the only time when collections could be secured satisfactorily was near mid-day on sunshiny days. The temperature in such cases apparently had little or no effect on the result of the collections. Table 2 shows the results of five typical late fall and winter collections in which the number of crayfish obtained is correlated with the time required to make the collection, the temperature of the water, and the presence or absence of sunshine. All of the collections included in the table were taken near the middle of the day.

In winter the size of collections furnishes a very good indication of the amount of activity of the crayfish population at the time the collections are made, since only those individuals which are active in the water, or are sitting unprotected on the stream bottom, or are concealed

TABLE 2.—RELATION OF SIZE OF COLLECTIONS IN WINTER TO TEMPERATURE AND SUNLIGHT

Date of collection	Number of individuals secured	Time required (hrs.)	Temperature of water (C.)	Character of day
Nov. 18, 1933	64	1½	4°	Sunshiny
Dec. 6, 1933	68	1½	6°	Sunshiny
Dec. 20, 1933	30	1¼	5°	Cloudy
Jan. 6, 1934	31	2	4°	Cloudy
Jan. 20, 1934	70	2	5°	Sunshiny

under small stones are likely to be taken with the seine. The crayfish which are buried in the mud or are concealed under large stones are not likely to be collected. Therefore, the close correlation of the size of collections with the presence or absence of sunshine which is shown in the above table indicates an equally close correlation of diurnal activity with sunshine.

The fact that *C. propinquus* is to some extent diurnally active, and the apparent close relation of its diurnal activity to sunshine is at variance with some of the literature on the activity of crayfishes. Chidester (1908) found *C. bartonius bartoni* negative to strong light and nocturnally active under laboratory conditions. Pearse (1910) says: "All crayfish are nocturnal in their habits. . . . . They come forth at night to search for food." Newcombe (1929) says: "During the day crayfishes are usually found at rest, ... while at night they are very active, since it is at this time that they go in search of food." However, Hay (1919) repeatedly observed *C. propinquus* feeding during the day under natural conditions, and the writer also observed individuals feeding during the day on a number of occasions, both in nature and in the laboratory.

No systematic field study was made during the present work to determine whether or not *C. propinquus* is nocturnally active under natural conditions. The individuals which were kept in laboratory aquaria, however, showed no greater tendency to be active at night than during the day. When the light was turned on at any hour of the night, they were almost always found to be sitting quietly on the sand at the bottom of the aquarium. This evidence, considered in connection with the fact that *C. propinquus* is to some extent at least diurnally active under natural conditions, and the further fact that it is undoubtedly positive to sunlight, would seem to indicate that there is no definite nocturnal rhythm of activity in this species.

THE LIFE CYCLE

Type of Life History

Ortmann (1906) divides the species of the genus Cambarus into two groups on the basis of the general type of life history which they follow. He calls these two types the "cool water type" and the "warm water type." The species of the "cool water type" breed and spawn practically the whole year around, while those of the "warm water type" have a restricted breeding season. *C. propinquus* belongs to the "warm water type."

The seasonal life history of species of this type conforms to the following general outline: a fall mating season, a spring spawning season, a spring or summer period during which the males are all second form (when the copulatory appendages have temporarily lost the hard texture,

sharp points, and peculiar sculpturing which ordinarily accompany the mating season). This period is followed by a change at some time during the spring or summer by which the males again become first form as a prelude to the fall mating season. Both changes of sexual form on the part of the males occur in connection with molts.

In the following sections, detailed observations on the life cycle of *C. propinquus* will be presented, and the relation of these observations to those recorded by previous observers on this and related species will be discussed.

The Earliest Young

Time of Appearance:—The young appear among the free-swimming population during a very short period in May or early June. In 1933 the first young were collected on June 7th (Graph 26). In 1934, however, they were taken three weeks earlier, on May 13th (Graph 46). This time difference can be attributed to the occurrence of a generally different type of spring season in 1933 and in 1934. The spring of 1933 was cool, cloudy, and rainy, so much so that in many cases the planting of spring crops was delayed from three weeks to a month beyond the normal time. The spring of 1934, however, was relatively warm and sunshiny.

The difference in the time of the appearance of the young was due to an increase in the length of time required to hatch the eggs, rather than to a delay in the laying of them. In 1933 the first egg-bearing females were found on April 8th, and the latest on May 21st, thus making a period of 43 days during which the females were carrying eggs. In 1934 the first egg-bearing females were found on April 7th, and the latest on May 6th, making a period of only 29 days during which the eggs were carried. These periods correspond in general to the time required for the eggs to hatch, since the juvenile population, when first found, and before any factors making for differential growth have had time to take effect, forms such a homogeneous group that it is obvious that its members must all have been spawned at approximately the same time.

Andrews (1904) found a similar variation in the time required for the eggs of *C. affinis* to hatch, depending on the temperature during the time when the eggs were being carried by the female. With higher temperatures he found that the eggs hatched in five weeks after being laid, while with lower temperatures a period of eight weeks was required.

Description of Young.—At the time of their first appearance in the quantitative collections the young *C. propinquus* measure from 3.9 to 6.1 mm. cephalothorax length. This is equivalent to a total body length of approximately 8 to 12 mm. This juvenile section of the population when plotted graphically (Graph 26) forms a simple, unimodal curve with a very narrow spread. This indicates that all of the juvenile indi-

viduals are approximately the same age and represent the same general degree of development.

These young differ from the adult in having a more sharply pointed rostrum; proportionally larger and more prominent eyes; more slender chelae; and a difference in color. Also, the young crayfishes at this time have not yet developed the external sexual characters to a point where any recognition of the sex in the field is possible. The annulus ventralis of the female is not yet distinct, and the first abdominal appendages in both sexes are apparently identical, being small, short, and thread-like, resembling in general the other pleopods, though smaller and shorter. Even at this time, however, the valley of the rostrum shows the median carina which is characteristic of the species. The general shape of the body and the relative proportions of the cephalothorax and abdomen are similar to those of the adult, and the young animal swims in the same manner as the adult.

Length of the Dependent Period.—No direct observations have ever been published on the length of time during which the young of *C. propinquus* are associated with the mother after hatching. No females bearing young were taken in the collections made by the writer during the spring of 1933, and Dr. John Mizelle who carried on the work of collecting for the writer during the spring of 1934 was able to secure only a single *C. propinquus* female bearing attached young. This individual was taken on April 21, 1934, in connection with a field trip of an elementary zoology class, but it died before reaching the laboratory. The brood of this female evidently were hatched at an abnormally early date, since the majority of the adult female population were still bearing eggs on April 28th, one week later.

There are very few references in the literature to the finding of *C. propinquus* females bearing young. Pearse (1910) records finding a single female of this species with young in Whitmore Lake, Washtenaw County, Michigan, on May 29, 1898. Hay (1919) speaks of finding "one very small one with its mother" on June 7, 1901, in Lake Maxinkuckee, Indiana. Smith in her unpublished records of *C. propinquus* taken in 1910 and 1911, lists the finding of only three females of *C. propinquus* bearing young in the field, and only three others which hatched their eggs in the laboratory. She records no measurements or other observations for these.

The scarcity of records for females of this species bearing young makes it seem probable that the young remain with the mother for a relatively short time, and that during that time the female remains in seclusion and inactive. These conclusions are borne out by the evidence from the present study.

In 1933, in the collection of May 6th, all of the adult females were bearing eggs. In the following collection of May 21st only two egg-bearing females were taken, and the majority of the former egg-bearing group were absent from the active population. In the next collection, taken on June 7th, these females had reappeared in the active population along with the free-swimming young. At that time all of the adult females had completed their molt, which takes place immediately after the young are shed.

In 1934 the circumstances were similar. On April 28th practically all of the mature females were found to be carrying eggs. On May 5th only one egg-bearing female was taken and most of the former egg-carrying group were absent. In the following collection of May 13th these adult females had reappeared and were newly molted. Only a few young were taken in this collection, however, probably on account of local environmental conditions which made them less active on that day or at the time of day when the collection was taken.

The absence of a major portion of the adult females from the collection taken just prior to the appearance of the season's young in the free-swimming population indicates that these females were inactive or were in seclusion at the time the collection was made, and that they were then probably either hatching their eggs or were bearing attached young. It seems most probable that in both years this collection was taken while hatching was still in progress, and at a time when it was nearing completion, since only a few females were found in the active population which were still bearing eggs. Therefore, we may consider the date of the collection as being approximately the date of the completion of hatching for the major portion of the season's young. And since in 1933 the members of the juvenile population were all found to be of approximately the same size and degree of development at the time when they appeared in the free-swimming population, we may safely assume that the majority of the young in 1933 were hatched just prior to May 21st, and in 1934 just prior to May 5th.

Between these dates and the time of the appearance of the young in the quantitative collections there was a period of 17 days in 1933 (May 21st to June 7th) and of 8 days in 1934 (May 5th to May 13th). These periods represent the approximate lengths of time during which the young were carried by the females, together with the time required for the adult females to complete their molt after the young were shed. Some idea of the length of time required by the females to complete this molt may be obtained from the records of Smith (1910-11). In a collection taken from the stream on June 2nd she found "no females with young and a few females molted." On June 6th she found "all females

molted." This gives a period of 4 days during which a majority of the adult females were passing through the molt.

If we subtract 4 days from the 17- and 8-day periods to allow for the completion of the molt by the females which had been bearing the young, we have left periods of 13 days and 4 days respectively. These periods should represent approximately the length of time that the young were carried by the females in 1933 and in 1934. However, since the dates which we have for hatching represent the time of the completion of the hatch, it seems more justifiable to conclude simply that the period during which the young remain with the mother in this species may vary from one week or less in favorable seasons, to about two weeks in extremely unfavorable ones.

This conclusion agrees with the information obtained by Steele (1902) and by Ortmann (1906) for *C. virilis* and *C. obscurus,* both of which are closely related to *C. propinquus.* Steele (1902) found that the young of *C. virilis* remain attached to the female for 9 days or more. Ortmann (1906), in giving the life history of *C. obscurus* says: "the period during which the young stay with the mother seems to be short. . . . . The young crayfishes probably do not remain with the mother much longer than a week."

Developmental Stage of Earliest Young.—In the literature on the group of the crayfishes the term "stage" is used somewhat loosely to indicate any life history period. It is more properly confined, however, to the period between any two molts. Therefore, it is equivalent to the more specific term "instar." Although the latter term is not ordinarily used in carcinological publications, it will be used in the present work because there is less likelihood of confusion in regard to its meaning, than is the case with the more general term "stage."

Somewhat varying results have been recorded in studies of different species of crayfish, pertaining to the particular instar represented by the earliest free-swimming young. Andrews (1907) found that the young of *C. affinis* remain under the abdomen of the female during the first, second, and most of the third instars, or until nearly 26 days old. At that time the larvae measured 8 mm. in total body length (corresponding to approximately 4 mm. cephalothorax length). He said of this third instar that "in general the young crayfish of this stage is now for the first time like the adult."

Andrews, therefore, believed that all Cambarus young are dependent during three instars. In further support of this theory he showed that the young of *C. diogenes* remain with the female until the third molt (through the third instar). In addition he quoted Faxon (1885) as having found the young of *C. clarkii, C. bartoni,* and *C. gracilis* still under the abdomen of the female and measuring from 7 to 10 mm. long.

Steele (1902), however, in studying the young of *C. virilis* found that the first ecdysis did not occur until 9 days after hatching. As a result of this molt the young crayfish lost most of their larval characters and assumed the general body form of the adult. They might leave the mother on occasion after this molt, but did not necessarily do so.

In describing the young *C. virilis* of this second instar, Steele said: "The rostrum is much lengthened and is no longer bent down between the eyes. The chelae have lost their recurved hooks. The abdomen and cephalothorax have assumed about the same relative proportions as in the adult. The appendages of the first abdominal somite have not yet appeared, although a minute swelling can be seen and the appendages will be set free after the next molt." In this second instar the young *C. virilis* measured 7 to 8 mm. body length (corresponding to 3.5 to 4 mm. cephalothorax length).

This description shows that the young *C. virilis* of the second instar are quite similar to the young *C. propinquus* which first appear in the quantitative collections. There are only two notable differences. One of these is the size of the young animals: 7 to 8 mm. body length for *C. virilis* as compared to 8 to 12 mm. body length for *C. propinquus*. The other difference lies in the fact that in Steele's *C. virilis* of the second instar the appendages of the first abdominal somite had not yet appeared, and did not appear until after the next (the second) molt, while in the young of *C. propinquus* when they first appear in the collections these appendages are present, though as yet they are undifferentiated. In view of these differences it seems probable that the young *C. propinquus* have already undergone two molts before they appear in the free-swimming population.

Conclusions Regarding Earliest Young.—On the basis of the foregoing observations it seems justifiable to conclude that: (1) the young *C. propinquus* remain with the mother for a relatively short time; apparently one week or less in favorable seasons, with the period extended to about two weeks in extremely unfavorable seasons; (2) that the females bearing young remain in seclusion, and are relatively inactive during the time that the young are attached; (3) that the young which first make their appearance in the quantitative collections are probably in the third instar, having left the mother at, or shortly after, the occasion of the second molt; and (4) that, in favorable years at least, these first two molts have occurred in rapid succession.

Sex Recognition

In the season of 1933 it was possible to recognize the sex of the juvenile population in the field for the first time in the collection of July

10th. This was more than a month after the season's young first appeared in the quantitative collections. At that time the young crayfishes measured from 6 to 16 mm. cephalothorax length, and the juvenile population had become divided into two size groups (Graph 28), each with a distinct mode. These two groups, however, were not separated on the basis of sex, for each group contained individuals of both sexes.

At the time when it was first possible to differentiate between the sexes, the first abdominal appendages of all the males were of the "juvenile" form. The two rami of each first abdominal appendage in the young males at this time were perfectly straight and parallel and were relatively uniform in thickness from base to tip. At the same time the ends were blunt and rounded, showing no hint of a point. The rami of the first abdominal appendages of adult "second" form males always show a tendency to be thicker at the base than at the tip, and have ends which are bluntly pointed rather than rounded.

The question has never been raised as to whether or not the "second" form of adult males is the exact equivalent of the "juvenile" form of the immature males, which is likewise usually referred to as the "second" form. Creaser (1933) states definitely that the "second" form is a developmental stage. Most writers, Faxon (1884), Harris (1901 and 1903), and Creaser (1933), have assumed that the two forms are identical, and that at times other than the breeding season the first abdominal appendages of mature males revert to the immature or juvenile condition. In view of the slight but constant differences just pointed out, it seems more justifiable to consider that the "second" form of adult males is only a partial equivalent of the "juvenile" form of young males, and that the reversion of the copulatory appendages of adult males after the breeding season is only a partial reversion in the direction of the juvenile condition.

Growth of the Juvenile Population

Increasing Range of Size.—During the summer, the spread between the largest and smallest members of the juvenile population increases progressively. Whereas in the June 7th collection (Graph 26) this "spread" amounted to only 2 mm. cephalothorax length, it increased to 6 mm. in the June 25th collection (Graph 27); 10 mm. in the July 10th collection (Graph 28); 13 mm. in the July 22nd collection (Graph 29); and 15 mm. in the August 31st collection (Graph 31). Similarly in 1932, the "spread" increased from 9 mm. in the collection of June 29th (Graph 4) to 14 mm. in the collection of September 15th (Graph 8).

This spread gives conclusive evidence of the establishment of individual differences in growth rate, and since growth in crayfishes is

conditioned by the molting process, there is a definite tendency for the growing population to become segregated into distinct groups rather than to vary at random.

Number of Size Groups.—The juvenile population forms a single unimodal size group (Graph 26) when it first appears. With the operation of differentiating growth factors during the summer this population becomes first bimodal and later polymodal. In the summer of 1933 the bimodal condition appeared in the collection of July 10th (Graph 28), a little more than a month after the juvenile population first appeared in the collections. In 1932 the juvenile population was already bimodal when the first collection was taken on June 29th (Graph 4) at the beginning of the present study. In these two apparently corresponding collections there were two major modes, and also a few individuals in advance of the more advanced of these two modes, forming a minor mode of their own.

During the summer the two major modes tend more and more to break up (compare Graphs 4, 5, 6, 7, and 8 for 1932; and Graphs 28, 29, and 30 for 1933) until finally in the late summer the population becomes definitely polymodal (Graphs 8 and 30). In both of the years during which the study was carried on the juvenile population came to exhibit five major modes, indicating the presence of five major size groups, at the end of the summer.

The first appearance of these five size groups among the juvenile population in 1932 was in the collection of July 27th (Graph 6). However, in this collection there were still two major groups. These were accompanied by three minor ones. Two of these minor size groups were in advance of the more advanced of the two major groups, and one was still less advanced than the less advanced of the two major groups. On August 11th, however, the five size groups were all well defined (Graph 7), and by September 15th (Graph 8) all traces of the two major size groups of summer had disappeared.

In 1933 the five major size groups first appeared in the collection of August 5th (Graph 30), and from that time on they maintained their identity more or less faithfully throughout fall and winter.

Constancy of Size Groups.—In both the 1932 and the 1933 populations these size groups could be identified, usually very prominently, in nearly all collections after they had become established. Sometimes one of them was represented by a mode affecting one sex only, either male or female, but the writer found, as did Creaser (1934), that the males and females exhibited no appreciable differences in the length of the cephalothorax, and that modes affecting only one sex could safely be used for drawing conclusions regarding size groups. Usually a size group repre-

sented only by a male or by a female mode in one collection would occur strongly in both sexes in the following collection. The same was true in cases where one size group was absent altogether from a collection. This happened occasionally, but in every case one of the later collections, usually the one immediately following, would show the group as strongly present as ever, and with a mode in the same place, or approximately the same place, as it had appeared previously. This was true in the case of the usual collections of 60 or more individuals, and it proved to be equally true in the mid-winter collections when it was sometimes impossible to secure more than 30 individuals on a collecting trip. Even in these small collections the five size groups usually maintained their identity perfectly.

This experience, borne out by two full years of collecting, led the writer to abandon all doubt as to the validity of the method of study.

Significance of the Size Groups.—Most of the records regarding the growth rate of young crayfishes have been taken from observations of single individuals, or, at most, of small groups of individuals. All such records have been secured under laboratory conditions. Smith (1910-11) found that in fifteen individuals of *C. propinquus* which molted in the laboratory, the increase in cephalothorax length accompanying the molt was 2 mm. in all but four cases. In three of these four cases the increase was 3 mm., and in the other case it was 2.5 mm. Andrews (1904) in studying the young of *C. affinis* found the following body lengths for the growing young: first instar, 4 mm.; second instar, 4.5 mm.; third instar, 8 mm.; fourth instar, 12 mm.; fifth instar, 15-18 mm.; sixth instar, 21 mm.; seventh instar, 29 mm. The average of the differences between these sizes is 4.9 mm. This represents the average increase in total body length accompanying a single molt. This is equivalent to approximately 2.45 mm. cephalothorax length. Therefore in the young of *C. affinis* which were studied by Andrews, the average increase in cephalothorax length was approximately 2.45 mm. for each of the first six molts.

In the present study it was found that the average distance between the modal points, both in the bimodal and polymodal conditions was 2.42 mm. In the majority of cases the distance was 2 mm., but in some cases it was 3 mm. or 4 mm. The size groups among the juvenile population, as represented by the modes, in both the bimodal and polymodal conditions, consist of groups of individuals within the population which have maintained approximately the same growth rate. The differences in size between the modal groups represent the average growth increment of each group over the group of next smaller individuals. In the light of the observations of Smith and of Andrews, it appears that the difference in size between any group, and the group immediately smaller, represents the average increment resulting from a single molt. Therefore, if a group

is advanced in size by 2, 3, or more millimeters beyond the one immediately to its left on the population graph, it is because the individuals of the first size group have undergone one more molt than the individuals of the immediately lesser size group. During that molt the individuals of the more advanced size group made an average increase in cephalothorax length of 2 mm., or 3 mm., or whatever may be the distance between the particular two modes in question.

We may safely conclude, then, that the distances between the modal points represent the average growth increments of different size groups as the result of single molts. On this basis the average increment resulting from a single molt among the juvenile population during their first season was 2.42 mm.

Therefore, the bimodal condition (Graph 28) bespeaks a population a part of whose members have undergone one more molt than the smaller individuals in the population. The presence of a very few individuals advanced in size beyond the more advanced of the two major size groups (Graph 4) gives reason for believing that these few individuals have undergone two more molts than the smallest members of the population.

Similar reasoning applied to the polymodal condition, showing the five major size groups found in the population at the end of the summer, leads us to believe that the members of the most advanced of these groups have undergone four more molts than the members of the least advanced group.

Size at the End of the First Growing Season.—At the end of the first growing season the largest individuals of the season's young may have reached a cephalothorax length of as much as 27 mm.; while the smallest individuals may have reached a cephalothorax length of only 12 mm. In the fall of 1932 the members of the largest of the five size groups ranged from 24 to 27 mm. cephalothorax length while those of the smallest of the five groups ranged from 13 to 16 mm. In the fall of 1933 the largest ranged from 22 to 26 mm., while the smallest ranged from 12 to 15 mm. The generally smaller size of all individuals of the young population at the end of the 1933 growing season which is thus apparent is a further effect of the retarded spring season and late hatching of 1933.

Differences in Growth Rate During the First Season.—If the average growth increment as a result of each molt during the first growing season (after the first two molts which are presumed to have occurred before the young appeared in the quantitative collections) is 2.42 mm. then the approximate number of molts undergone during the first growing season may be ascertained by the following formula:

$$\frac{x-y}{2.42}+2=z$$

x = mode of the size group in question at the end of the season.
y = mode of the juvenile population when it first appears in the quantitative collections.
2.42 = the approximate average growth increment with a single molt.
2 = number of molts undergone by the young crayfishes before they appear in the quantitative collections.
z = total number of molts undergone.

For greater accuracy, x should represent not simply the mode of the size group in question for a single collection taken at the end of the season, but rather the average of the extreme ranges which the mode of the group may occupy as ascertained by repeated collections taken at intervals over a considerable period after the growing season has ended. The mode of the first appearing juvenile population is used for y rather than the average for that population, because any expression of the average in round numbers would be identical with the mode.

Thus, in the case of the largest size group in the population at the end of the 1932 growing season (24 to 27 mm.):

$x = 25.5$
$y = 5$ (This is taken from the mode of the juvenile population when it first appeared in the quantitative collections on June 7, 1933. This number is probably a constant).

Therefore: $\frac{25.5 - 5}{2.42} + 2 =$ approximately $10 =$ total number of molts or z.

In the case of the second size group from the right on the graph (the second most advanced), by similar calculation the number of molts undergone would be approximately 9. In the case of the third size group from the right (the third most advanced) it would be approximately 8. For the fourth size group it would be approximately 7, and for the fifth size group approximately 6.

Thus the young crayfishes which are hatched in May or June pass through 6 to 10 molts during the first growing season with an average increment of 2.42 mm. cephalothorax length (equivalent to approximately 5 mm. total body length) with each molt. By mid-September they measure 12 to 27 mm. cephalothorax length which is equivalent to approximately 24 to 54 mm. total body length.

Other writers on the group of the crayfishes have recorded similar differences in growth rate among the juvenile population. Andrews (1904) in his work with *C. affinis* noted wide differences in growth rate among the season's young. "During these 2 months and 3 weeks of summer," he says, "some few seem not to have grown at all, while about a third of them have almost doubled their length." Writing again in 1907 he estimates that the young of *C. affinis* pass through 11 to 13

instars during their first summer; but he says that in some cases the young crayfishes may be only 20 mm. long in the fall, due apparently to their development being arrested during the 6th instar. He gives the body lengths of 101 specimens of *C. affinis,* which he raised in laboratory aquaria, as being 20 to 62 mm. in the October following their first growing season.

Ortmann (1906) in his life history of *C. obscurus* says that the young crayfishes hatched in May or June measure 26 to 50 mm. body length by the end of September. He says: "It seems that the rate of growth of young crayfishes is very different in different individuals, some gaining through June, July, August, and September only about 15 mm. in length, others more than twice that length."

Creaser (1934) writing of *C. propinquus* in Michigan, says that the season's young attain a size of 10 to 20 mm. cephalothorax length by September. This is equivalent to a body length of 20 to 40 mm.

Thus in every case in which the growth of young crayfishes during the first season has been observed, it has been found that the rate of growth differs greatly among individuals and that therefore the spread between the largest and smallest individuals or groups in the population increases during the summer and reaches a climax in late September or early October at the close of the growing season.

Causes of the Differences in Growth Rate.—Although all students of the group of the crayfishes agree as to the remarkable differentiation in size which takes place during the first season among the originally homogeneous juvenile population, only Andrews (1907) attempts to account for it. He suggests that insufficient food may be the cause of the lack of growth on the part of the smaller individuals. In speaking of one brood of laboratory-reared crayfishes which averaged 50 mm. body length in the fall as against an average of 41 mm. for the entire group reared in the laboratory, he attributes the advanced size of this brood to its having had more food and possibly also more favorable conditions of temperature than the remainder of the group. In another connection he says, "the rate of growth was very different in individuals, and in some cases seemed to depend directly upon food supply."

Andrews' specimens were all carried through the first growing season in the laboratory, and the reasons which he gives for the retardation of the growth of a portion of them as compared to the rest are more applicable to laboratory-reared crayfish than they are to crayfish which grow up under natural conditions. In the natural environment temperature as a cause for retardation of growth is ruled out as all members of the juvenile population are subjected to approximately the same temperature conditions. Shortage of food is likewise not likely to affect any portion of the population except in abnormal seasons, since in the locality which

was studied by the writer, there was more than abundant food for all the crayfish there, both young and old.

It seems to the writer that the differences in rate of growth are more probably due to inherent genetic growth factors than simply to environmental causes. The invironmental conditions undoubtedly influence the expression of these inherent genetic factors, however, and probably determine the upper limit of size which may be attained in a particular season. This was apparently the case in 1933, when the retarded spring season resulted in the attainment of a smaller total size in the case of all groups than in the preceding season of 1932.

Attainment of Sexual Maturity

Sexual Form of Males at the End of the First Season.—Until the end of the summer the males of the season's young remain in the juvenile form. During August and the first half of September, however, there is a progressive change from the juvenile condition to the first form. Table 3 shows the progressive change in form among the young males during the late summer and early fall of 1932.

Table 3.—Progressive Change of Form of Young Males

Date of collection	Total number of young males	Number in juvenile form	Number in first form
Aug. 11, 1932	23	23	0
Sept. 15, 1932	14	8	6
Sept. 26, 1932	28	16	12
Oct. 6, 1932	51	8	43

After the beginning of October, in 1932, the first form males continued to outnumber the juvenile males among the season's young in most of the collections taken during the fall and winter. This condition of the juvenile population probably represents the normal fall and winter condition at this latitude.

In 1933 the results were less conclusive. In two collections taken during September and October (Sept. 20th and Oct. 7th) the first form males outnumbered the juvenile males among the young of the season. In the other fall and winter collections the number of juvenile males exceeded the number of first form males by a ratio which was in most cases approximately two to one. It seems probable that in the fall and winter of 1933 the number of juvenile males really exceeded the number of first form males among the season's young at all times, and that the two collections in which the opposite was true were the result of inaccurate sampling. Such a conclusion is in accord with the results of the

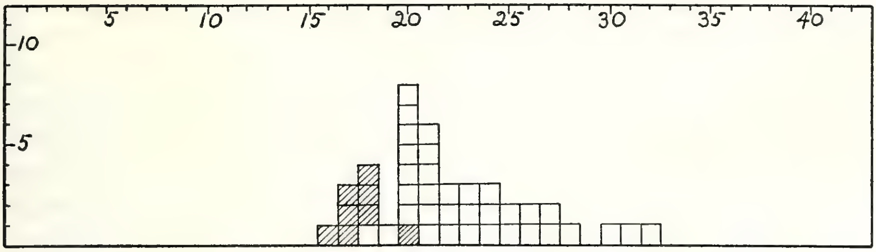
majority of the fall and winter collections of 1933-34, and also with the generally delayed appearance of all crayfish life history phenomena in the season of 1933.

A similar relation of the length of the growing season to the percentage of males of the young of the year which reach maturity by the first fall is evident in the work of Creaser (1933) and of Smith (1911) with *C. propinquus.* Creaser working with this species at Ann Arbor, Michigan, where the growing season is necessarily shorter than at Urbana, Illinois, found that some males of the season's young became first form by the beginning of fall, but that the great majority of them did not do so. Smith, in a collection taken at Douglas Lake, Michigan, on Aug. 5th found that among 16 young males, 4 were first form and 12 were still juvenile. In a collection recorded for the same day taken at Urbana there were 30 young males, 21 of which were first form and 9 juvenile. Thus in collections taken on the same day, the majority of the young males in the Michigan population were still juvenile, while the majority of those in the Illinois population had already become first form. Therefore, apparently the longer growing season characteristic of the more southern location not only enables a higher percentage of the young males to reach maturity by the end of their first growing season at Urbana, Illinois, than in central Michigan, but also causes the young of the Urbana population to show greater advancement at any particular time during the late summer.

Investigators working on other species of crayfish have likewise found that a portion of the young of the year reach maturity by the end of the first season. Ortmann (1906) in the study of the closely related species, *C. obscurus,* in Pennsylvania found that most males of the season's young become first form by October. With *C. affinis,* also, Andrews (1904) found that in Maryland a portion, at least, of the young males attain maturity by the beginning of the first fall after they are hatched.

Size of Males at Sexual Maturity.—It was found in the present study that a cephalothorax length of 20 mm. marked approximately the boundary between sexual maturity and immaturity among the males of less than one year. The individuals measuring 20 mm. and above were generally found to be first form, indicating that they had attained sexual maturity, while those that measured less than 20 mm. were generally immature. This division however was by no means absolute. Individuals which had reached sexual maturity below 20 mm. were not uncommon, and occasional individuals were found which had passed this size and were still immature.

The accompanying distribution curve (Graph 1) represents sexual maturity in males in a winter collection which was typical of the collections taken after the end of the growing season. The unshaded portions



GRAPH 1.—Showing the distribution of sexual maturity among the males in a typical winter collection (February 18, 1933). The shaded squares represent the immature, and the unshaded squares the mature individuals. The abscissa represents cephalothorax length in millimeters.

of the graph represent the mature males, and the shaded portions represent the immature males. In this graph the fact that an approximate boundary between maturity and immaturity exists at 20 mm. cephalothorax length is plainly apparent.

First form males below 18 mm. cephalothorax length were exceedingly rare, although one was taken on November 17, 1932, which was only 12.6 mm. The largest immature male taken measured 23.1 mm. cephalothorax length. This individual occurred in the collection of November 3, 1932. True second form males of a much larger size than this were found between the first and second adult molts of the adult males in the spring, but in the opinion of the writer a distinction may properly be made between the juvenile condition of the copulatory appendages, and the true second form condition as it occurs in adult males. Therefore these large second form males cannot be placed in the same class as the immature males.

The boundaries of sexual maturity among the males of *C. propinquus* which were indicated in the present study agree with those recorded for the same species by Smith (1910-11). In her work, as in that of the writer, 20 mm. cephalothorax length formed an approximate lower boundary for sexual maturity among the males. She found that the great majority of first form males measured 20 mm. or more, and she found no first form males at all below 17 mm.

Ortmann (1906) found a similar size limit in *C. obscurus*. He found that in this species a body length of 40 to 50 mm. (corresponding to a cephalothorax length of approximately 20 to 25 mm.) was indicative of sexual maturity among the males. The smallest first form male that he found measured 38 mm. body length (approximately 19 mm. cephalothorax length).

A slightly different result, however, was obtained by Creaser (1933) in his study of the *C. propinquus* of Michigan. If we may judge by his graphs, he found a much greater percentage of first form males measur-

ing below 20 mm. cephalothorax length than occurred in the studies of either Smith or the writer. Indeed, in his collections, the size of 20 mm. seems to be totally without the significance which it was found to have in the Illinois population. The size of 16 mm. or 17 mm. would apparently hold something of the same significance in Creaser's collections. This difference between the results of Creaser and those obtained by Smith and the writer for the Illinois population is largely explainable on the ground that Creaser's population represented a smaller race of *C. propinquus* than that found in eastern Illinois. This theory finds support in the fact that Creaser's largest adults rarely exceeded 30 mm. cephalothorax length, whereas in the race of crayfish used in the present study, a portion of the yearling adult group regularly exceeded 30 mm., and the absolute maximum of size seemed to be between 35 and 40 mm. Creaser's crayfish seem, therefore, to have averaged from 3 to 5 mm. smaller in cephalothorax length among all size classes than the Illinois crayfish.

Sizes of Females at Sexual Maturity.—There is no available criterion for determining whether or not individual females among the young of the year are sexually mature at the end of their first growing season. However, a general idea of the boundary of sexual maturity among the young females can be obtained by observing the sizes of the females seen in copulation during the fall. In the present study no females below a cephalothorax length of 20 mm. were found copulating, but apparently females of 20 to 25 mm. cephalothorax length (all young of the season) were quite as likely to be taken in copulation as were older and larger individuals.

Similar results were obtained by Smith (1910-11). She also found copulation taking place with females of as low as 20 mm. cephalothorax length, undoubtedly belonging to the young of the season. Likewise in the closely related species, *C. obscurus,* Ortmann (1906) observed copulation in the fall among the sexually mature individuals of the season's young, the smallest female taken in copulation having a body length of 43 mm. (approximately 21 mm. cephalothorax length).

A further and more general criterion for sexual maturity among the females is furnished by the size of the females found bearing eggs in the spring. The evidence from this source fully verifies the existence of an approximate lower limit of sexual maturity among the females at 20 mm. cephalothorax length. Thus apparently with females as with males, this size forms the approximate boundary of sexual maturity among the young of the year in the race of *C. propinquus* found in eastern Illinois.

Copulation

In connection with the present study pairs of *C. propinquus* were taken copulating or in copulatory attitude in the months of September, October, November, and March. Smith (1910) found copulating crayfish of this species in the field at Urbana, Illinois, in October, November, and December; and at Douglas Lake, Michigan, in July and August. Hay (1919) found *C. propinquus* copulating in Lake Maxinkuckee, Indiana, in November, January, and April. Turner (1926) gives the date of September 1st in Michigan and August 25th in Wisconsin for the observation of copulation in *C. propinquus.* Creaser (1933) says that in the vicinity of Ann Arbor, Michigan, the mating season of the species is in October and November.

Thus it seems that the occurrence and duration of the mating season of *C. propinquus* varies widely with the locality. In more northern latitudes, such as Michigan and Wisconsin, it probably begins in July and August, and lasts until November, but does not occur again in the spring.

In more southern latitudes such as east-central Illinois and Indiana it probably begins in September and lasts until the onset of severe winter weather in December or January, then begins again in March, and may last into April. It is possible that with mild winter temperatures such as occur in some years, the mating season might last throughout the winter at the latitude of Urbana, because males will attempt to copulate at any time during the winter if warmed and placed in close confinement with females.

This corresponds to the experience of Pearse (1910) who found that male crayfish during the mating season will attempt copulation almost immediately if placed in close confinement with females, and also to the experience of Bell (1906), who found increased sexual activity among the males accompanying a rise in temperature.

In copulating pairs the male and female are usually approximately the same size, although occasionally the writer has seen larger males attempting to copulate with smaller females in laboratory aquaria. Creaser (1934) says: "Presumably only a small percentage of females can mate as young of the year, unless the males are polygamous, because observations indicate that mating pairs are of about the same size." The writer during two years of observation saw nothing to indicate that male crayfish are necessarily monogamous, and Andrews (1895) says definitely that in *C. affinis* conjugation may be repeated by either animal with some other individual.

Static Condition During the Fall and Winter

After the latter part of September or the early part of October growth ceases in all cases. In the present study the latest date at which a "soft," freshly molted individual was taken was October 6th. This individual was a young female and measured 17.1 mm. cephalothorax length.

In the collections taken during the fall and winter the five size groups in the population of the young of the year remain distinct and maintain relatively constant levels of size. In the different collections the mode of each group may vary back and forth within a range of 2 to 4 mm., but in all cases the five modes representing the five size groups maintain the same general relations to one another (Graph 3).

The variation in the position of each mode is indicative of the operation of two factors: (1) the individual variation among the members of each size group, and (2) the vagaries of sampling. Consistently larger collections might have produced less variable results.

Other investigators have likewise found a cessation of growth in the early fall, and a static condition of the population during the fall, winter, and early spring. Andrews (1907) says of *C. affinis:* "After October there are no more molts until the following warm season, the lengths remaining constant through the winter." Ortmann (1906) says that in *C. obscurus* the winter is passed without change. According to Creaser (1934) there is no growth among the *C. propinquus* of Michigan after about September 24th. And Turner (1926) writing of crayfish in general says: "During the winter, growth . . . . is at a low ebb, and no molting takes place."

In all cases this absence of molting may be easily seen from the condition of the exoskeleton. In all crayfish, large and small, taken in the winter collections, the shell is dark, almost black, and is frequently covered with algal and protozoan growths.

Creaser (1934) advanced the theory that the cessation of growth and molting in the early fall might be caused by falling temperature, and he related this to the fact that at Ann Arbor, Michigan, he observed no crayfish feeding during the winter months. It seems probable that the phenomenon may be related to falling temperature, although in 1933, at Urbana, during the period in which the cessation of growth was noticed the days were still warm, with temperatures ranging from 15° to 20° Centigrade. The temperature control, however, if such it is, must operate in some way other than to cause the crayfish to stop eating, for the writer found food in the process of digestion in the stomachs of *C. propinquus* taken in December. Furthermore, the crayfish are relatively active for six weeks after growth has ceased in the fall, and Hay (1919) reports seeing

crayfish of this species feeding regularly during October and the first half of November in Lake Maxinkuckee, Indiana.

It seems likely that the gradual lowering of the mean temperature for the 24-hour period which takes place during the early fall, largely on the account of the occurrence of cooler nights, may cause a slowing of the physiological processes of the animals to a level of mere maintenance, thereby bringing about a cessation of growth and molting.

This seems particularly probable in view of the fact that recent studies such as that of Markus (1933) on the relation of temperature to the rate of digestion in the black bass, have shown that in cold blooded forms a very close correlation exists between temperature and the rates of physiological processes.

Spring Reproductive Activities

Kinds of Activity.—Except for the occurrence of copulation in the spring in some localities the reproductive activities of spring concern the females only. They consist of two distinct phases: (1) the laying and carrying of the eggs, and (2) the hatching and carrying of the young.

It was necessary to treat fully the second phase of the female reproductive activities, that is, the hatching and carrying of the young, at the beginning of this study, in connection with the appearance of the first young of the season. The first phase of these activities, however, the laying and carrying of the eggs, although it was necessarily mentioned in connection with the hatching of the young, is more properly considered at this point in the description of the life cycle, since it is directly related to all of the events which take place among the adult female group at this time.

Egg Laying.—During a part of the month of March the adult females are largely absent from the active population. Table 4 shows the ratio of males to females for two typical winter-time collections, two collections taken during the month of March, 1933, and two taken during the month of April, 1933. The purpose of the inclusion of the two winter collections in the table is to show the normal sex ratio as a basis for comparison

Table 4.—Sex Ratio in Winter and Spring Collections

Date of collection	Males	Females	Percent males	Percent females
Jan. 26, 1933	35	24	60	40
Feb. 18, 1933	42	33	56	44
Mar. 4, 1933	56	20	74	26
Mar. 18, 1933	51	15	77	23
Apr. 8, 1933	29	22	57	43
Apr. 22, 1933	32	29	52	48

with the March collections when the females were largely absent, and the April collections when they have rejoined the active population.

From Table 4 it is seen that the males outnumber the females normally to a slight extent. This ratio in favor of the males, however, markedly increases during the month of March, and returns to normal shortly after the beginning of April.

The first females bearing eggs appear coincident with the return of the adult females to the active population in early April. In 1933 the first egg-bearing females were taken in the collection of April 8th. In 1934 they appeared in the collection of April 7th.

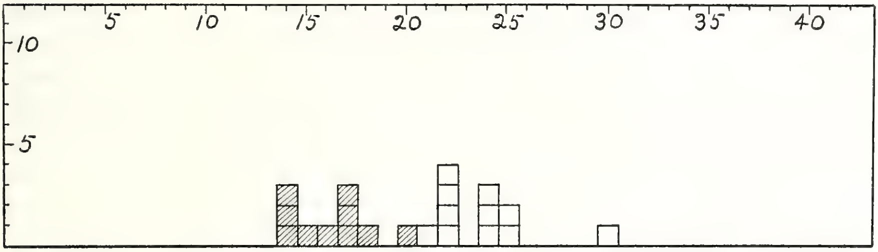
High water handicapped the work of collecting during the month of March in both years, so that a proper search for the missing females could not be made. However, since most of them reappear in early April, bearing eggs, it may be reasonably assumed that their absence during March is connected with the laying of the eggs. Andrews (1895 and 1904) tells of the extreme excitability of the females of *C. affinis* as egg-laying time approaches. It is reasonable to suppose, then, that during the egg-laying period and for some time prior to it the females remain hidden and inactive. Therefore, we reasonably may consider that the eggs in *C. propinquus* are laid in late March or early April, and that most of them are laid at about the same time, since the disappearance and reappearance of the females takes place *en masse*. One female, however, of sexually mature size was found without eggs on April 22, 1933, and on examination it was discovered that a normal clutch of well-developed eggs were still internal, having not yet been laid. Whether this female would have laid later, or whether she would have produced young at all, cannot be determined. However, no young were found in either 1932 or 1933 which bore evidence of belonging to so late a hatch as this would have been.

The conclusion that the eggs of *C. propinquus* are laid in late March or early April at Urbana, Illinois, corresponds closely to the results of Smith (1910-11) for this species in the same location, and also to the results of Ortmann (1906) for the related species *C. obscurus* in Pennsylvania. Smith found the first females with eggs on March 25th. Ortmann found no egg-bearing females on March 28th or March 31st, but found numerous ones on April 6th. In the work of these investigators, as in that of the writer, the eggs apparently were laid in almost all cases at practically the same time.

Egg Carrying.—During the two years of the present study, females bearing eggs were taken only during the months of April and May. Egg-bearing females were present in the collections of April 8th, April 22nd, May 6th, and May 21st, 1933; and of April 7th, April 28th, and May 5th,

1934. After the initial appearance of egg-bearing females practically all sexually mature females were found with eggs.

These results again agree closely with those obtained by other investigators. Smith (1910-11) found practically all sexually mature females of *C. propinquus* carrying eggs on April 29th, and collected the last egg-bearing female on May 18th. Pearse (1910) took *C. propinquus* females with eggs at Walnut Lake, Oakland County, Michigan, on May 2nd, and June 6th; at Coldwater, Michigan, on April 17th; and at Ann Arbor on April 18th. Creaser records 15 females of this species as being taken with eggs near Dexter, Michigan, on May 24th.



GRAPH 2.—Showing the distribution of egg-carrying among the females taken in the collection of April 8, 1933. The shaded squares represent females not carrying eggs and the unshaded squares those carrying eggs. The abscissa represents cephalothorax length in millimeters.

Thus the egg-bearing season for *C. propinquus* apparently lasts during the month of April and a part or all of the month of May in the latitude of Urbana, Illinois, and probably lasts from mid-April to early June in the more northern latitude of Michigan.

Size of Females Carrying Eggs.—The lower size limit of the females bearing eggs corresponds to the general lower size limit of sexual maturity among both males and females, as ascertained at the time of copulation in the fall. Here again the cephalothorax length of 20 mm. forms an approximate boundary, separating, in this case, those females which bear eggs from those which do not.

In the accompanying graph (Graph 2) of the female population taken in the collection of April 8, 1933, during the egg-bearing season, this boundary is clearly evident. The shaded portions of the graph represent those females which were not carrying eggs at the time the collection was made. The white portions represent the egg-bearing females. This graph represents the condition of the female population typical of the egg-bearing season.

The occurrence of females below 20 mm. cephalothorax length with eggs was rare. Such females were taken occasionally, however. The

smallest female found with eggs measured 16.1 mm. cephalothorax length, and was taken on May 6, 1933. The largest female taken without eggs during the egg-bearing season measured 24.9 mm. cephalothorax length and occurred in the collection of April 28, 1934.

Smith (1910-11) obtained results with *C. propinquus* similar to those of the present study. She found no egg-bearing females measuring less than 18 mm. cephalothorax length. Likewise, Ortmann (1906) found 40 mm. body length (approximately 20 mm. cephalothorax length) to be the lower size limit of egg-bearing among females of *C. affinis*.

Creaser (1934), however, obtained somewhat different results with the Michigan race of *C. propinquus*. He records the cephalothorax lengths of 14 egg-bearing females as follows: "one each, 15, 16, 17 and 18 mm.; five 19 mm.; and one each: 20, 21, 23, 24 and 25 mm." Here the size boundary of 20 mm. cephalothorax length appears to be without significance. This is in accord with the results which he obtained concerning the size of the young males at the time of attainment of sexual maturity, and it may likewise be explained by assuming that Creaser was working with a generally smaller race of *C. propinquus* than that occurring at Urbana, Illinois.

Number of Eggs Carried by the Females.—The numbers of eggs carried by the females were found to be roughly proportional to the sizes of the individuals. The largest female taken with eggs measured 36.1 mm. cephalothorax length and had an estimated clutch of 175 eggs. The largest clutch, estimated at 250 eggs, was borne by a female measuring 31.4 mm. cephalothorax length. The smallest female which was found bearing eggs measured 16.1 mm. cephalothorax length and had an estimated clutch of 40 eggs. The smallest number of eggs found on any female was 5, and occurred on a female measuring 21.7 mm. cephalothorax length. In this case, however, as in a number of other cases showing only a few eggs, the manner in which the eggs were scattered on the pleopods gave evidence that the few eggs were only the remains of a larger clutch, the majority of which had been lost.

Smith (1910-11) records additional evidence which shows that the number of eggs carried is in general proportional to the size of the individual female. She found a female measuring 38 mm. cephalothorax length which was carrying 225 eggs, and another measuring 20 mm. cephalothorax length, and carrying 102 eggs. These cases agree essentially with the results obtained in the present study.

Spring Molts of the Yearling Group

Criterion for Determining the Occurrence of First Molts.—The collector has no difficulty in determining which individuals among the cray-

fish taken in the spring collections have undergone a molt and which have not done so. Up to the time of their first molt in the spring the shells of all of the crayfishes of both sexes, whether large or small, retain the dark color characteristic of the winter season. They frequently retain also the encrusted algal and protozoan growths which accumulate during the winter.

Number of Molts Among the Mature Yearling Males.—There have been various observations recorded by a number of investigators concerning the number of molts undergone by male crayfishes during the second season after they are hatched. In most species which have what Ortmann (1906) called the "warm water type" of life history, it has been found that the adult males undergo two molts during their second season. The first of these has been generally called the "spring" molt, while the second molt has been variously called the "summer" or "fall" molt, depending on the time of its occurrence. It will be shown in this study that during one of the years in which the investigation was carried on, this second molt of the adult males occurred so early in the season that it did not even justify the use of the term "summer" molt. Therefore it has seemed best in the present study to refer to these molts as the first and second adult molts of the males.

Both of these molts involve changes of the form of the first abdominal appendages on the part of the adult males. These males have passed through the winter with first abdominal appendages of the first form. They become second form as a result of the first adult molt and then revert back to first form as a result of the second adult molt.

The First Adult Molt of the Mature Yearling Males.—The first molts among the adult males in the spring appear in April or May. In 1933 the first newly molted males of this group appeared in the collection of May 6th. Out of 21 adult males taken on that day 5 were newly molted. In 1934, however, the first newly molted adult males appeared in the collection of April 7th, along with the first egg-bearing females. At that time, out of 63 adult males, 22 were molted.

It seems probable that the occurrence of the first adult molt in 1934 was more nearly normal than that in 1933, since the laying of the eggs by the females, and the new molts of the males represent correspondingly initial spring activities on the part of the two sexes. Also, it is well to remember again in this connection that the spring of 1933 was very much retarded while the spring of 1934 was relatively normal.

The first adult male molt occupies a relatively short period of time. In 1933 the first molted individuals of this group were discovered on May 6th and at the time of the next collection on May 21st all adult males were molted. In 1934 the first newly molted adult males were taken on

April 7th, and before the time of the next collection on April 28th, all had completed the molt.

Smith (1910-11) gives a slightly later date for the occurrence of the first adult male molt in *C. propinquus* than was recorded during either of the years of this study. She gives the date for its occurrence as being from May 13th to June 2nd. However, in view of the wide divergence found in the time of the occurrence of this molt as between the two years of the present study, this still later period given by Smith may easily be accounted for by the particular character of the season during which she worked.

Workers on other species of crayfish have obtained results similar to those obtained by Smith and by the writer for *C. propinquus*. Steele (1902) places the first adult molt for the males of *C. virilis* in Missouri from early April to mid-May. Ortmann (1906) says that with *C. obscurus* in Pennsylvania the first adult molt of the males takes place in most individuals during the first half of May, but that some individuals may begin as early as March.

In both *C. virilis* and *C. obscurus*, therefore, as well as in *C. propinquus*, the first adult male molt in the spring in most cases is accomplished sometime during the months of April or May. Undoubtedly in the case of a species like *C. propinquus* which occurs over a wide territory this molt takes place at a relatively later date in the more northern locations. And in all cases the earliness or lateness of the occurrence of the molt in any particular area is certainly dependent on the character of the season.

Second Adult Molt of the Mature Yearling Males.—After the completion of the first adult male molt in the spring there are no first form males in the population, since all of the males which had previously been first form became second form at the time of the first adult molt. Any first form males which occur in the late spring or early summer, therefore, are those which have also completed the second adult molt, since it is by this molt that the adult males again become first form.

In the writer's study of *C. propinquus* in 1932, a collection taken on June 29th showed 11 first form males and 9 second form males. Since these first form males had unquestionably completed the second adult molt it is evident that this molt was well advanced at that time. In the next collection, taken on July 14th, 4 first form males were taken, and one second form male. In all later collections taken during the summer all adult males were first form. It seems justifiable to conclude, therefore, that in 1932 the second adult male molt began in the latter part of June and was completed in nearly all cases by the middle of July.

In 1934 the second adult molt of the males was apparently a "second spring molt" rather than a "summer molt." On April 7th, 41 first form

males (still retaining their old winter shells) were taken along with 22 second form (newly molted) males. These second form males were all adult in size and had become second form with the first adult molt of spring. Apparently therefore, this collection was taken just in the middle of the first adult molt of the season. At the time of the next collection, taken on April 28th, all the adult males had lost their old winter shells, indicating that they had all passed through the first adult molt, and 7 out of 38 had also passed through the second adult molt, and become first form again. The remaining 31 males were still second form. Just one week later, on May 5th, only 7 males out of a total of 62 remained second form, all others had completed their second adult molt and become first form.

Thus apparently in the season of 1934, both first and second adult molts took place within a little more than a month among most of the adult male group of the population. Presumably at some time during the month of April, there was a short period during which all adult males were second form. Then, just before the collection of April 28th the second adult molt began, and it was largely completed by May 5th, just one week later.

It seems probable that the remaining second form males which had not yet undergone the second adult molt by May 5th did so during the remainder of May or in the early part of June. The second form males present in the collections of June 29th and July 14th, in the summer of 1932 probably represented such "stragglers" which underwent the second adult molt and changed to first form somewhat later than the majority of the adult male group.

Smith (1910-11) was unable to find evidence of any second adult molt at all among the males of *C. propinquus* in the Urbana population. This may now be explained on the basis that in the spring of 1911, as in that of 1934, the two molts occurred very close together. If this were true, she might easily have confused the two, and thought them a single extended molting period.

Apparently the occurrence of the second adult male molt among the *C. propinquus* of Michigan is more delayed, judging from the work of Creaser (1933) and of Smith (1910-11). Creaser's graph for a population sample taken on July 30th indicates that the second adult molt was largely finished by that time, since the adult males taken were mostly first form. These had mostly been second form in his graph for June 29th, showing that at that time the first adult molt had occurred but not the second. Smith found that all adult males were still second form at Douglas Lake, Michigan, on July 6th. On August 5th only one second form male of adult size was found, all the others having reverted to first form. Thus, in Michigan the second adult molt of the males must occur during July and early August.

Investigations on other species of crayfish have generally demonstrated that the second adult male molt occurs in summer rather than in spring. Steele (1902) says that this molt occurs among the *C. virilis* of Missouri between June 10th and July 1st with most individuals. Ortmann (1906) found that the second molting season for adult males began in July and lasted until late September, or early October, among the Pennsylvania population of *C. obscurus.*

The occurrence of the second adult molt of the males at so early a date as that recorded in the spring of 1934 for *C. propinquus,* at Urbana, has never been established for any other species of crayfish. It is impossible to say whether or not such an early occurrence of this molt is normal with this species at this latitude. It seems probable, however, that the second adult molt among *C. propinquus* may occur early in this way, whenever the season is sufficiently favorable.

Molting Among the Immature Yearling Group.—Those individuals among the previous year's generation of young which failed to attain sexual maturity by the end of the first growing season and which passed through the winter and spring in the immature state undergo their first yearling molt at the same time as the first adult molt of the males. Two females and one male of immature size were found newly molted along with the newly molted adult males on May 6, 1933. They also undergo a second yearling molt at the same time as the second adult molt of the males.

With the first yearling molt the immature males do not change the form of the copulatory appendages, but retain the juvenile form. With the second yearling molt, however, these immature males attain sexual maturity and become first form. Therefore, after this molt all yearling males in the population are first form. Presumably the immature females also become mature with this second yearling molt since they attain adult size as a result of it.

There is evidence that the members of this immature group also undergo a third and a fourth yearling molt during the summer.

This is in accord with the statement of Creaser (1933) who says: "Between March 17th and June 29th the young of the previous year resume their growth, rapidly increasing to adult size, probably by reason of several moltings." Creaser's "young of the previous year" were for the most part immature during the fall and winter, so their behavior would in general parallel that of the immature section of the previous season's young in the present study.

The Spring Molt of the Adult Females.—The adult females which have borne eggs during the spring, undergo only a single molt. This takes place immediately after the young are shed. In 1933 the first newly

molted adult females were found on May 21st. At the time of the following collection, taken on June 7th, the entire adult female population had molted. In 1934 the first newly molted adult females were found in the collection of May 5th, and in the following collection, taken on May 13th, all were molted.

Smith (1910-11) obtained similar results. She secured the first molted adult females on June 2nd, and found that the entire adult female group had completed its molt by June 6th.

Growth Among the Yearling Group

Growth Among Mature Yearling Males and Immature Individuals.—Since the first and second yearling molts of the immature group occur at the same time as the first and second adult molts of the yearling males, these groups may be considered together in the matter of growth during the two molts. In both years of the present study there was apparently no growth among either the adult yearling males or the immature group as a result of the first molt. Examination of the composite graph (Graph 3) shows that the lines representing all size groups, both mature and immature, remain essentially level during and following the time of this molt.

In contrast to the result of the first molt, the second molt of the adult males and immature individuals results in marked growth among both groups. The growth increment accompanying this molt varies from 3 mm. cephalothorax length in some individuals to as much as 8 mm. in others. The variation among individuals as to the amount of growth which accompanies this single molt stands in marked contrast to the condition prevailing during the juvenile growth period of the first growing season. Among the juvenile population differences in size apparently come about for the most part as a result of differences in the number of molts undergone rather than as differences in the amount of growth increment following a single molt. The distinctness of the size groups which were formed in the late summer among the juvenile population as a result of the differences in the number of molts undergone by different groups of individuals depended upon the fact that the individuals within each group had not only passed through the same number of molts, but had also undergone approximately the same amount of growth at the time of each molt.

As a result of the wide individual variation in growth rate in the spring at the time of the second yearling molt, there is a tendency for individuals to "migrate" into other size groups more advanced than their own, thus bringing about a "piling up" of individuals in the more advanced size groups at the expense of the less advanced ones. (Compare Graphs 25 and 26 for 1933, and Graphs 45 and 46 for 1934.)

The fact that the growth increment accompanying this molt was as much as 8 mm. cephalothorax length in some cases, while it was never more than half this much in the case of the juvenile molts of the first season is very interesting in view of the fact that there was apparently no growth at all in connection with the first yearling molt. Presumably the approximately doubled growth which takes place in some individuals at the time of the second yearling molt compensates for the absence of growth at the time of the first yearling molt.

The only published reference to the occurrence of a molt without growth in any species of crayfish is that recorded by Creaser (1933). He mentions the possibility that young males, at the end of their first growing season in the autumn, may molt without increase in size in case they undergo a change from the juvenile condition to the first form during the molt. In the present study, however, the molt without growth occurred in the spring and involved: (1) mature first form males which underwent a change to second form at the time; (2) juvenile males which remained in the juvenile form after the molt; and (3) immature females. Therefore, the case is in no way parallel to the one given by Creaser.

No full explanation of the absence of growth in connection with the first molt of spring can be offered at the present time. However, a consideration of the nature of the growth process in crayfish suggests a possible explanation. Since growth among crayfish is periodic, the anabolic processes between molts result in the accumulation of substances which are stored in the body as additions to the protoplasmic content and as stored food; but because of the physical limitations imposed by the integument the body does not increase in size until the confining shell is cast off. Then chiefly through imbibition of water the newly molted individual increases in size, reestablishing temporarily the equilibrium between formed substances and water content of the body. It seems probable that in the late winter and early spring physiological activity is reduced to a minimum because of the low temperature of the water. Under such conditions there would be no appreciable accumulation of substances. Therefore at ecdysis the imbibition of water would be negligible, and consequently with the first molt of spring there would be no appreciable change in size. Such an explanation seems particularly plausible in view of the fact that a correlation between temperature and physiological activity is probably the cause of the cessation of growth and molting among the crayfish population in the fall.

The third and fourth yearling molts of the immature group apparently result in about the same growth increment as was found to be characteristic of the juvenile molts (2 to 4 mm. cephalothorax length). These

two molts, however, and the growth accompanying them will be considered further in connection with the accounts of their occurrence.

Growth Among the Mature Females.—The second yearling molt of the adult males and the immature individuals occurs at approximately the same time as the single molt of the adult females. This molt involves growth among the adult female population of the same general extent and character as that which takes place in connection with the second yearling molt of the other two classes.

Thus the major portion of the growth among the yearling population takes place at approximately the same time in both sexes and in all size groups, although the molt by which it is accomplished among the adult females does not correspond to the one by which it is accomplished among the members of the other two classes.

Attainment of Maximum Size

As a result of the growth occurring in connection with the second yearling molt of the adult males and the single molt of the adult females, the entire yearling adult population reaches a size of 25 to 35 mm. cephalothorax length (Graphs 26 and 46). At the same time the size groups which were immature during the winter and spring attain a cephalothorax length approximating or exceeding 20 mm. (Graphs 26 and 46) and become sexually mature.

The 25 to 35 mm. cephalothorax length seems to constitute for the great majority of the race the maximum size which an individual may attain. During two years of observation and collecting, a small number of *C. propinquus* were taken which measured more than 35 mm. cephalothorax length. These individuals apparently represented special cases of survival and growth beyond the ordinary maximum size characteristic of the race. On June 29, 1932, a single male was taken which measured 40 mm. cephalothorax length. This was the largest individual ever found, and apparently represented the extreme upper limit of size for the race of *C. propinquus* occurring at Urbana, Illinois.

Death of the Yearling Adults

Almost immediately following the second adult molt of the yearling males and the single molt of the adult yearling females, resulting in the attainment of the ordinary maximum size by these classes, the major portion of this adult population of both sexes completely disappears. In the collections taken after the middle of June, members of the maximum size groups are almost wholly lacking.

There remain three classes of individuals in the collections taken in

late June and early July (Graphs 27 and 28): (1) the young of the season, most of which are still below 12 mm. cephalothorax length; (2) a small adult group, measuring about 23 to 30 mm. cephalothorax length; and (3) occasional individuals measuring from 35 to 40 mm.

Apparently all or nearly all of the individuals of both sexes which were sexually mature during the winter and spring, and which produced the year's generation of young, die following the molt by which they attain maximum size. This phenomenon is clearly shown in the graphs representing the collections for June 7th and June 25th, 1933 (Graphs 26 and 27). In the collection of June 7th the adults of the winter and spring are still present in the population, measuring from about 25 to 35 mm. cephalothorax length. The immature individuals of the winter and spring, which now have become adult, all measure 19 mm. or more, and these, because of greater individual growth in a large number of cases, show a tendency to "pile up" on the adult population, thus shortening the range of the yearling group as a whole.

In the following collection, taken June 25th, the large adults are entirely absent, and the major portion of the entire yearling group has disappeared. There remain, besides the young of the season, only a few adult individuals which measure from 23 to 30 mm. cephalothorax length.

This condition continues relatively the same during the remainder of the summer. At no subsequent time does the large adult group reappear in the samples, as would be the case if they had gone into burrows or had migrated to other parts of the stream. Furthermore, a careful search made in holes in the bank along the water edge and in other parts of the stream revealed none of them.

Therefore we cannot escape the conclusion that, in the season of 1933, between June 7th and June 25th, most of the large adults died, including the major portion of the entire adult population, and that portion which produced most of the season's generation of young. The small adult group in the collection of June 25th, which ranges from 23 to 30 mm. cephalothorax length, apparently represents a portion, at least, of the group of individuals which passed through the winter and spring in the immature condition, and only became mature following their second molt in the spring. These individuals have apparently passed through a third molt, involving an increase in size of about 4 mm. cephalothorax length, between June 7th and June 25th, since on June 7th the smallest of them measured 19 mm. while on June 25th the smallest of them measured 23 mm. Definite evidence for the occurrence of this molt was found in connection with the collection of June 25th. In this collection two "soft," freshly molted females were taken which measured 25.4 and 28.3 mm. cephalothorax length, and which therefore belonged to the surviving yearling group.

Probable Nature of Adult Death

In the habitat under consideration *C. propinquus* plays a relatively important rôle in food chains. Fishes are the most important natural enemies of this species. During the present study no attempt was made to evaluate the effects of predators on the crayfish population. The progressive changes which take place in the crayfish population as the season advances, however, give no evidence of marked alteration attributable to the action of predatory species. Therefore it seems probable that the toll exacted by predators is a fairly uniform one, being relatively the same at all seasons, and affecting all classes of the population equally.

The death which decimated the adult population was undoubtedly a natural death, since no observed catastrophe took place which would account for it; and the fact that it affected only one class of the population precludes the possibility of its having occurred as a result of disease. Furthermore, it was not peculiar to the season of 1933, since a similar event had apparently taken place in 1932 before the first collection was taken on June 29th, judging from the size of the adult group in the four summer collections of 1932 (Graphs 4, 5, 6, and 7).

The occurrence of natural death in this species cannot be laid to the attainment of the ordinary maximum size alone, because the members of the small, remaining, yearling adult group, which measure from 23 to 30 mm. cephalothorax length in June, all attain the ordinary maximum size later in the summer, and survive at this size through the fall, winter, and the following spring. Therefore there must be some other factor which, occurring in conjunction with maximum size, acts as a contributing cause in bringing about natural death. Since natural death apparently involves only those individuals which have not only attained the ordinary maximum size, but which have also contributed to the production of the season's young, the coincident occurrence of parenthood and maximum size offers the basis for the most plausible theory regarding the immediately contributing factors which bring about their death.

The occurrence of natural death among adult crayfishes of maximum size coincident with the close of the reproductive season has been recorded previously by four different investigators. Creaser (1933) found natural death occurring among the adult males of *C. propinquus* in Michigan after the breeding season. Chidester (1912) likewise mentions the death of adult males after the breeding season in *C. bartonius bartoni*. He says that "in the spring the males die off in great numbers." Andrews (1904), writing of *C. affinis* in captivity, says: "After sexual union many died, and it was found that the males died in larger numbers than the females." Ortmann (1906) says concerning *C. obscurus:* "Another remarkable fact is that after the end of the molting season in spring no

very large males are found." He believes that the large males die, and describes in detail two cases in which he found males of the maximum size in a dying condition and yet bearing no injury of any kind. He believes it probable that the old females die in the same manner as the males, since they are entirely absent from the population after the young are shed at the beginning of summer.

The records of these investigators apparently bespeak conditions which were at least partially parallel to those found by the writer. The observations of Ortmann, in particular, afford an interesting comparison with the results of the present study, in view of the fact that *C. obscurus* and *C. propinquus* are closely related species. The fact that all four investigators found natural death occurring particularly among the males, parallels the fact that the writer found a marked excess of females among the small group of "oversize" individuals measuring from 35 to 40 mm. cephalothorax length. This is especially notable in view of the fact that in the population as a whole there was a definite preponderance of males.

The Summer Adult Group

The small group of individuals which survived the decimation of the adult population and which measured from 23 to 30 mm. cephalothorax length in the collection of June 25th (Graph 27) are represented regularly in the summer collections. These individuals were apparently those members of the yearling group which passed through the fall, winter, and spring in the immature condition, and which attained adulthood only at the time of their second yearling molt. Therefore they did not contribute to the production of the season's brood of young. They molted twice at the time of the first and second adult molts of the mature males in the spring and apparently molted again during the month of June.

By the early part of August these individuals have all attained the ordinary maximum size of 25 to 35 mm. cephalothorax length. Therefore they evidently undergo a fourth molt during late July or early August, involving a growth of 2 to 4 mm. cephalothorax length. Evidence for the occurrence of this fourth molt was obtained in two cases during the present study. The writer collected two "soft," freshly molted females, measuring 25.3 and 28 mm. cephalothorax length, on July 27, 1932. And in a collection taken for the writer on August 5, 1933, another "soft" female was taken, which measured 28.5 mm. cephalothorax length. All three of the individuals in question belonged to the yearling adult group.

This group, therefore, enters the fall at the ordinary maximum size, and lives at this size through the winter and spring. The individuals belonging to the group copulate in the fall, along with the mature members of the season's generation of young. The females of the group bear

eggs in the spring and produce young. Creaser (1933) expressed the opinion that the two-year-old males in the population of C. *propinquus* which he studied did not change into second form. In the Illinois population, however, the two-year-old males undergo the two spring molts along with the adult yearlings, changing to second form with the first spring molt and reverting to first form with the second. The females likewise undergo the single spring molt along with the adult yearling females. Most individuals of both sexes among the two-year-old group apparently undergo an increase of 2 mm. or more in cephalothorax length in connection with the second adult male molt and the adult female molt (Graphs 26 and 46). This gives to all of the individuals of this group a cephalothorax length of more than 30 mm., and to some of them more than 35 mm. Thus a portion of the group come to exceed the ordinary maximum size characteristic of the race.

Following these molts most of the individuals of this group die, along with the yearling individuals which have attained the ordinary maximum size and produced young. A very few of them, however, apparently survive and furnish the occasional "oversize" individuals, measuring 35 to 40 mm. cephalothorax length, which occur scatteringly in the collections throughout the year. At this size they apparently may survive through a third summer, fall, and winter, and escape natural death until the end of their third spring. During the two years of the present study only 34 individuals of this extreme size were taken, 21 of which were females and 13 were males. This unbalanced sex ratio apparently indicates that, among the two-year-old group at least, the factors which bring about natural death are more potent among males than among females.

This establishing of a differential death rate, leading to an elimination of males at an age earlier than that established for females of the same species, is in direct accord with the discovery of Van Cleave and Lederer (1932) who found that males of the snail *Viviparus contectoides* normally die shortly after reaching one year of age, while females normally attain the age of two years, and a few pass beyond the three-year limit.

Age Attained by Different Groups and Number of Broods Produced

On the basis of the evidence drawn from the present study we may conclude that the majority of the C. *propinquus* in the Illinois population produce a single brood of young and die as yearlings. This holds true for those individuals which grow rapidly and reach sexual maturity by the end of their first growing season.

Those which fail to reach sexual maturity by the first fall after they are hatched, pass through the winter in an immature state and reach sexual maturity at the beginning of their second summer. They survive

through the second year and, after producing a single brood of young in their second spring, most of them die as two-year-olds.

A very few individuals, however, among which the females greatly outnumber the males, survive through a third year and die at the end of their third spring. It was impossible to ascertain whether or not these individuals produced more than one brood of young during their lives. The members of this size class copulated in the fall, and the females were taken with eggs in the spring, so that they were certainly fertile. There is a possibility, however, that this class may consist of individuals which were immature during their first year, and failed to produce a brood during their second year, thus not bearing their single brood of young until the spring of their third year. If this is true, then the individuals of this species never produce more than a single brood of young, and die soon after it is liberated. If the 35 to 40 mm. individuals form an exception to this rule it still remains true for the great majority of the race.

The common impression among most writers has been that all crayfish live normally to an age of three years or more. Andrews (1907) kept some *C. affinis* which had been hatched in the laboratory until they were more than three years old, and he believed that some very large individuals of this species found in the field might be six or seven years old. Ortmann (1906), after extensive field study of *C. obscurus,* concluded that the normal life span of the individual in this species was about three years. Turner (1926) on the basis of these studies gave four years as the approximate life span of crayfish in general.

The results obtained by Creaser (1934), however, on *C. propinquus* form a conspicuous exception to the conclusions of these earlier workers and agree very well with the results of the present study when due allowance has been made for the shorter growing season occurring in Michigan, where Creaser worked, as compared to Illinois where the present study was conducted.

Creaser found that most of the season's young in the Michigan population failed to become mature by the first fall after they were hatched, and that most of the yearling individuals survived into the second year. The majority of the yearling group in the Michigan population, being immature, corresponds to the small yearling group in the Illinois population which failed to become mature by the first fall, and which apparently survived into a second year. Therefore the survival of the majority of the yearling group in the Michigan population into the second year is a result which would be expected on the basis of the findings of the present study.

Large numbers of the yearling individuals in Creaser's population died during the fall or early winter of their second year. A similar though less marked mortality was noticed among members of the cor-

responding age group in the present study accompanying the onset of winter, and the greater mortality in the Michigan population may have been due to the more severe winter in the more northern latitude.

Furthermore, although Creaser does not mention the fact in his paper, the graphs representing his collections show indications of the presence of a few very large individuals corresponding to the occasional individuals of 35 to 40 mm. cephalothorax length which were found in the present study. This class is represented in Creaser's population by individuals measuring from 30 to 35 mm. cephalothorax length. This smaller size corresponds to the generally smaller size of the Michigan race of *C. propinquus* as compared to the Illinois race of the same species.

Thus the *C. propinquus* which Creaser studied, like those studied by the writer, probably die a natural death as yearlings, if they have reached sexual maturity by the first fall after they are hatched; and do not die a natural death until two years old if they have failed to reach sexual maturity by the first fall. Likewise occasional individuals among them probably live to be three years old. Apparently, therefore, Creaser's crayfish, like those studied by the writer, with few exceptions, if any, produce only a single brood of young during their lives.

Thus the question of the length of life of the individuals in this species seems to be quite definitely linked to the two factors of rapidity of growth and reproduction. Ortmann (1906) says: "Whether slow growth, including late development, influences total length of life cannot be ascertained." However, in view of the indications of the present study, supported by the evidence of the similar study made by Creaser in a different locality, having different climatic conditions, the conclusion seems inescapable that the two principal factors which determine length of life in this species are: (1) the rapidity of growth, influencing as it does the time of attainment of sexual maturity; and (2) the engaging in the reproductive activities themselves.

Summary of the Life Cycle

We may summarize the life cycle of *C. propinquus* as it occurs in east central Illinois as follows: The young are hatched in May or June, and remain attached to the mother for about one to two weeks, depending on the season. Following the second molt they become free-swimming and possess in general the form of the adult. At this time they measure about 5 mm. cephalothorax length.

They undergo a total of six to ten molts between the time of hatching and the end of the first growing season in late September or early October. By the end of the season they reach a size of 12 to 27 mm. cephalothorax length. The majority of them attain sexual maturity at this time, since the attainment of sexual maturity coincides

in general with the attainment of a size of approximately 20 mm. cephalothorax length.

Copulation occurs during the late fall and early spring and involves individuals of less than one year old if they are sufficiently large to be sexually mature. During the winter no molting takes place and the sizes of all individuals remain unchanged.

The eggs are laid in late March or early April, and are carried for a period of four to six weeks depending on the temperature. The females remain in seclusion during the period when the eggs are being laid, and also while the young are attached.

The adult males molt twice during the spring, changing from first form to second form with the first adult molt, and from second form back to first form with the second adult molt. The immature yearling group, both males and females, molt twice at the same times as the adult males, then a third time during May or June, and a fourth time in July or August. They attain sexual maturity as yearlings at the time of their second molt in the spring. The adult females molt only once. This molt occurs just after the young are shed in May or June.

No growth takes place among the adult yearling males or the immature group as a result of their first molt of spring, but a very marked growth in both groups accompanies the second spring molt. A similar growth accompanies the single adult female molt.

As a result of this growth the adult yearling males and females attain the ordinary maximum size of 25 to 35 mm. cephalothorax length. Immediately following the attainment of this size they die a natural death. This natural death involves all of the yearlings of both sexes which were adult during the winter and spring. Therefore it involves the majority of the yearling group.

The members of the yearling population which only attained maturity as yearlings survive during a second year. They attain the ordinary maximum size of 25 to 35 mm. cephalothorax length as a result of their third and fourth yearling molts. They produce a brood of young as two-year-olds, and most of them die at the beginning of their third year, along with the adult yearlings; but a very few, among which the females greatly outnumber the males, live over a third year. These individuals attain a size of 35 to 40 mm. cephalothorax length, which apparently constitutes an absolute maximum of size for the race.

The great majority of this species, therefore, die as yearlings. A small section of the population survives during a second year, and occasional individuals live to be three years old. All the available evidence indicates that most or all individuals of both sexes produce only a single brood of young.

CONCLUSIONS

Environmental Relations

1. The young *C. propinquus* live in the surface water of the stream during most of their first summer.
2. The adults are bottom-dwellers at all seasons.
3. Members of all size groups seek the deeper portions of the stream during the winter.
4. Individuals of this species are positive to sunlight at all seasons.

Life Cycle

1. The young are hatched in May or June and remain attached to the mother about one to two weeks, during which time they probably undergo two molts.
2. At the time they become free-swimming they measure about 5 mm. cephalothorax length.
3. They undergo a total of 6 to 10 molts during the first growing season, and attain a cephalothorax length of 12 to 27 mm.
4. Sexual maturity in both sexes is attained coincident with a cephalothorax length of about 20 mm.
5. The majority of the season's young normally attain sexual maturity by the first fall after they are hatched at the latitude of Urbana, Illinois.
6. During the winter no growth or molting takes place and the sizes of all individuals remain unchanged.
7. Copulation occurs during the late fall and early spring at the latitude of Urbana, Illinois.
8. The eggs are laid in late March or early April, and are carried for a period of 4 to 6 weeks, depending on the temperature.
9. The adult males molt twice during the spring or early summer, changing to second form with the first adult molt, and reverting to first form with the second adult molt.
10. The immature yearling group of both sexes apparently molt four times during their second year. They attain sexual maturity with the second yearling molt.
11. The adult females undergo a single molt immediately following the shedding of the young in the spring.
12. Apparently no growth takes place in connection with the first yearling molt, among either mature males or immature individuals; but marked growth occurs in connection with the second yearling molt in both groups.
13. A similar growth takes place as a result of the single molt among the adult yearling females.

14. The portion of the young of the previous year which reached sexual maturity by the end of their first growing season, produce a brood of young the following spring, attain maximum size as a result of the second adult molt of the males and the single adult molt of the females, and die as yearlings.

15. The group which failed to attain maturity by the end of their first growing season live over a second year; attain maximum size during their second summer, produce a brood of young in their second spring, and for the most part die as two-year-olds.

16. A very few individuals, among which females predominate, survive over a third year, and produce a brood of young in their third spring.

17. With the possible exception of the few which live to be three years old, the individuals of this species apparently produce only a single brood of young during their lives.

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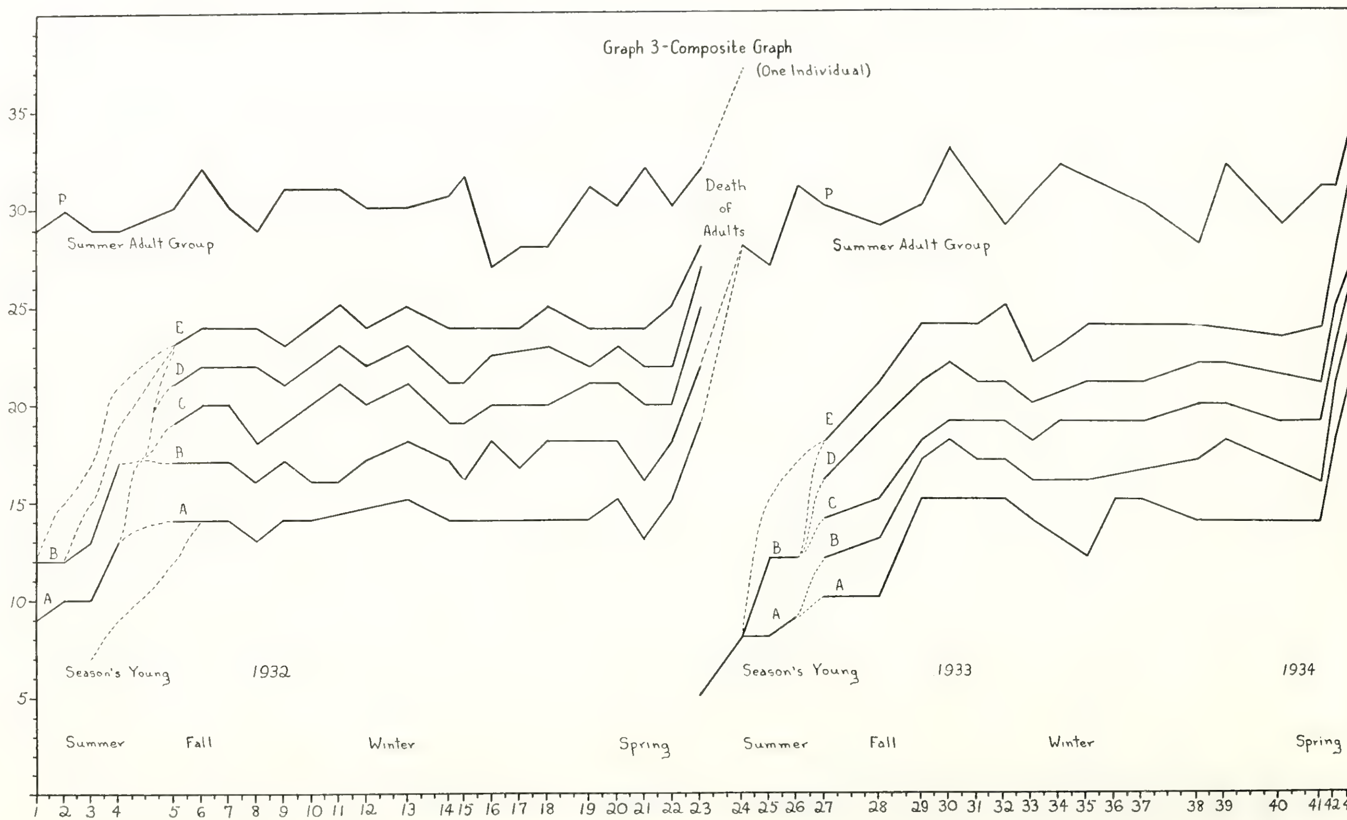
GRAPHS

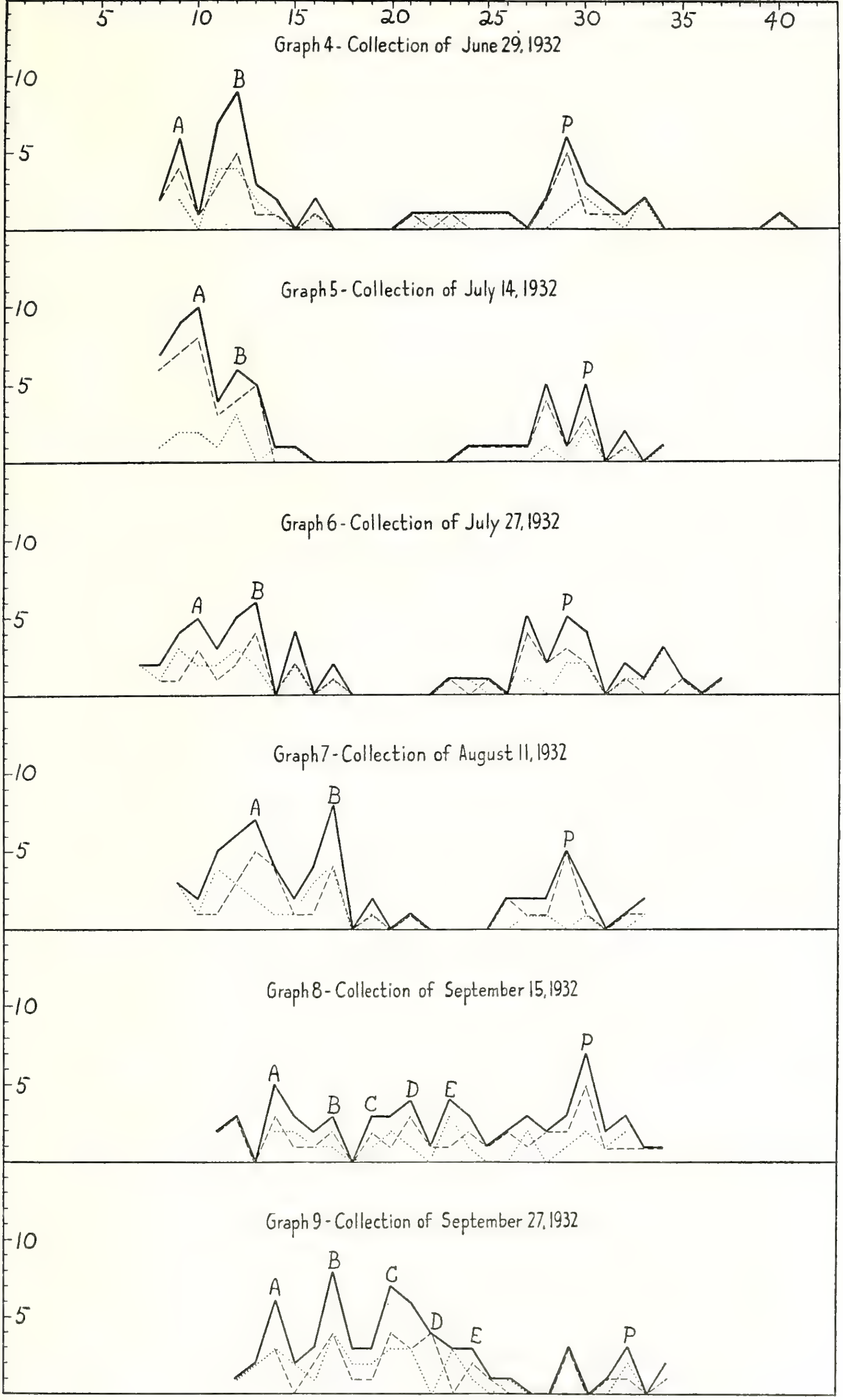
The collections taken during the two years in which this study was in progress are represented by the following series of forty-four graphs. Of these, forty-three (Graphs 4 to 46, inclusive) represent individual collections, arranged chronologically. On these graphs the abscissa represents cephalothorax length in millimeters, and the ordinate represents number of individuals; the total population is indicated by a solid line, the females by a broken line, and the males by a dotted line.

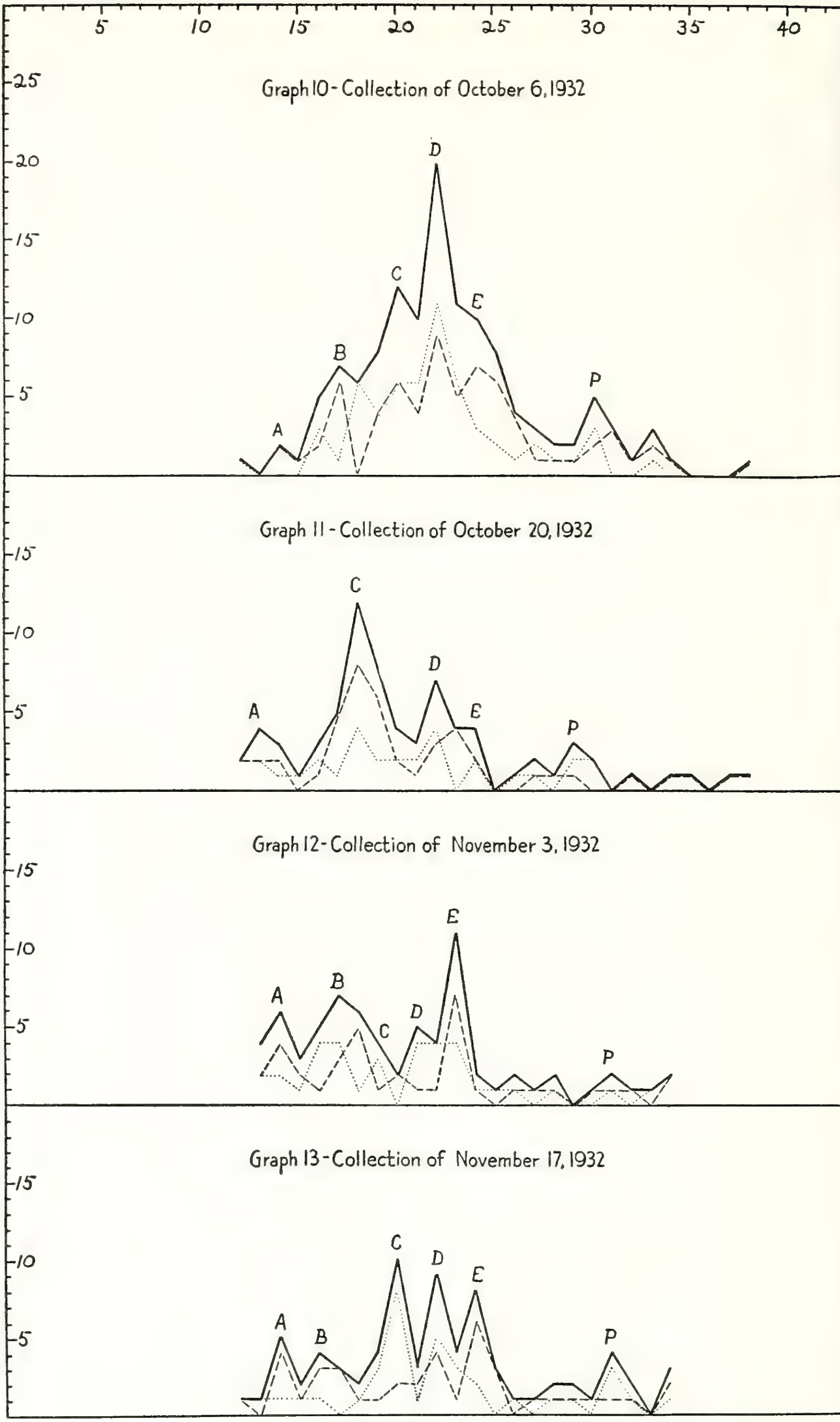
The first graph of the series (Graph 3) is the composite graph, showing the progress of the modes, representing the size groups. The abscissa represents time in weeks, while the ordinate represents the position of the modes in millimeters. The letters A, B, C, D, E, and P on the lines of this graph refer to the corresponding letters on the modes of the graphs of individual collections. Each line on the composite graph thus represents the development and history of a particular size group in the population. Each number on the abscissa represents a single collection. In the following list the dates of the collections are given with the corresponding numbers shown in Graph 3:

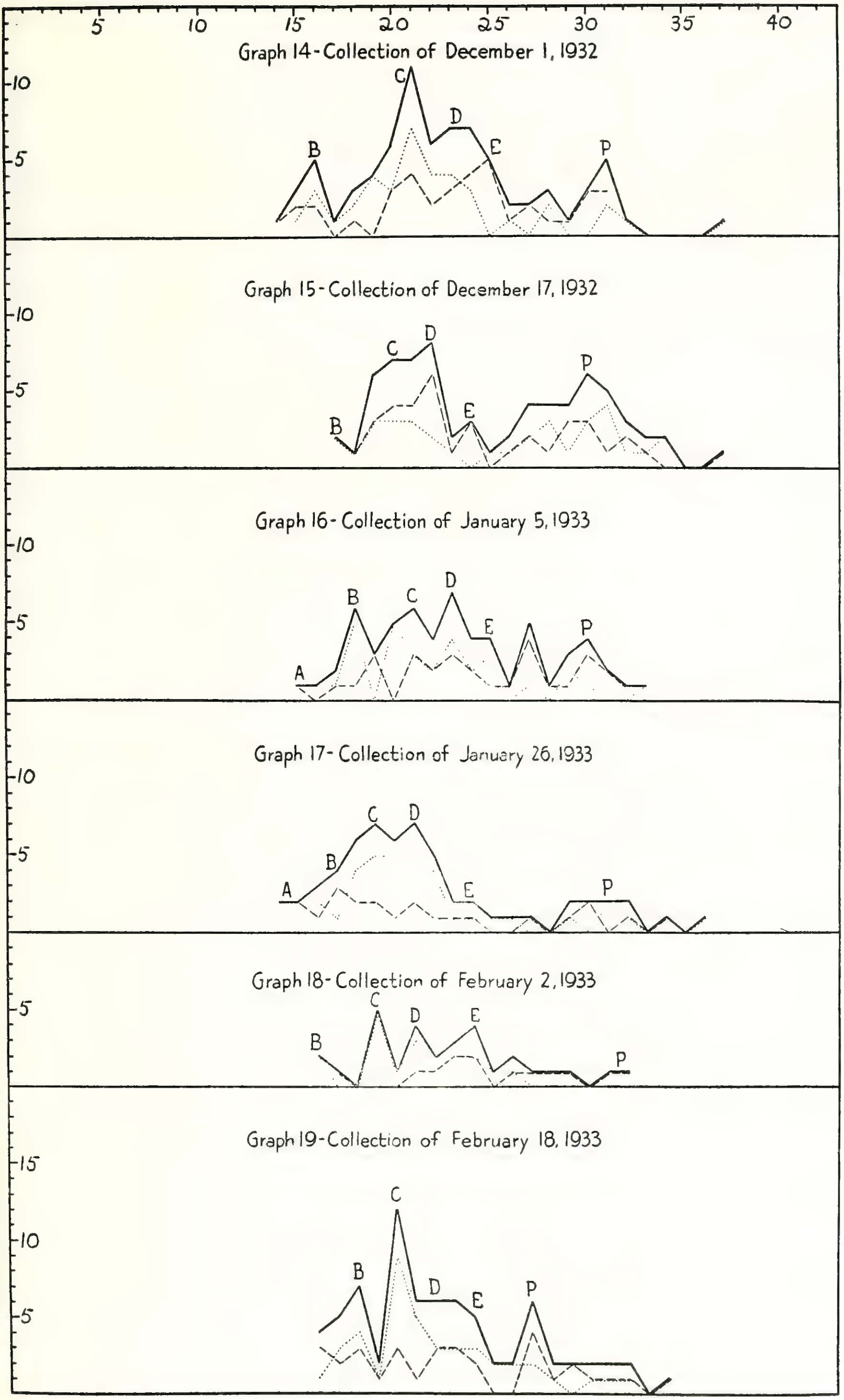
1. June 29, 1932
2. July 14, 1932
3. July 27, 1932
4. August 11, 1932
5. September 15, 1932
6. September 27, 1932
7. October 6, 1932
8. October 20, 1932
9. November 3, 1932
10. November 17, 1932
11. December 1, 1932
12. December 17, 1932
13. January 5, 1933
14. January 26, 1933
15. February 2, 1933
16. February 18, 1933
17. March 4, 1933
18. March 18, 1933
19. April 8, 1933
20. April 22, 1933
21. May 6, 1933
22. May 21, 1933
23. June 7, 1933
24. June 25, 1933
25. July 10, 1933
26. July 22, 1933
27. August 5, 1933
28. August 31, 1933
29. September 20, 1933
30. October 7, 1933
31. October 24, 1933
32. November 4, 1933
33. November 18, 1933
34. December 6, 1933
35. December 20, 1933
36. January 6, 1934
37. January 20, 1934
38. February 17, 1934
39. March 4, 1934
40. April 7, 1934
41. April 28, 1934
42. May 5, 1934
43. May 13, 1934



For explanation see page 57.


5 10 15 20 25 30 35 40
Graph 4 - Collection of June 29, 1932
Graph 5 - Collection of July 14, 1932
Graph 6 - Collection of July 27, 1932
Graph 7 - Collection of August 11, 1932
Graph 8 - Collection of September 15, 1932
Graph 9 - Collection of September 27, 1932


5 10 15 20 25 30 35 40
25 20 15 10 5
Graph 10 - Collection of October 6, 1932
A B C D E P
15 10 5
Graph 11 - Collection of October 20, 1932
A C D E P
15 10 5
Graph 12 - Collection of November 3, 1932
A B C D E P
15 10 5
Graph 13 - Collection of November 17, 1932
A B C D E P


5 10 15 20 25 30 35 40
Graph 14 - Collection of December 1, 1932
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B C D E P
Graph 15 - Collection of December 17, 1932
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B C D E P
Graph 16 - Collection of January 5, 1933
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A B C D E P
Graph 17 - Collection of January 26, 1933
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Graph 18 - Collection of February 2, 1933
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B C D E P
Graph 19 - Collection of February 18, 1933
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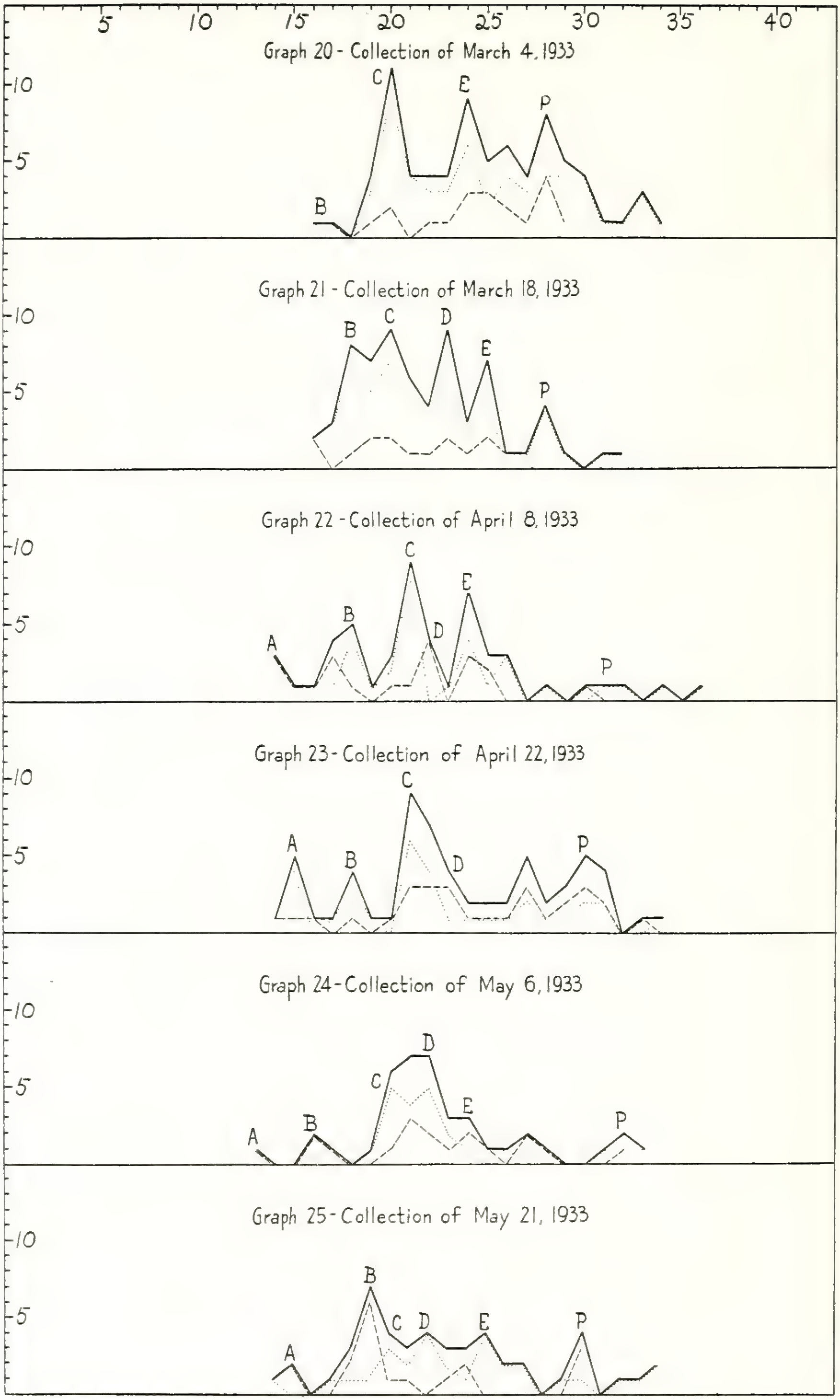
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Graph 20 - Collection of March 4, 1933
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Graph 21 - Collection of March 18, 1933
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Graph 22 - Collection of April 8, 1933
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Graph 23 - Collection of April 22, 1933
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Graph 24 - Collection of May 6, 1933
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Graph 25 - Collection of May 21, 1933
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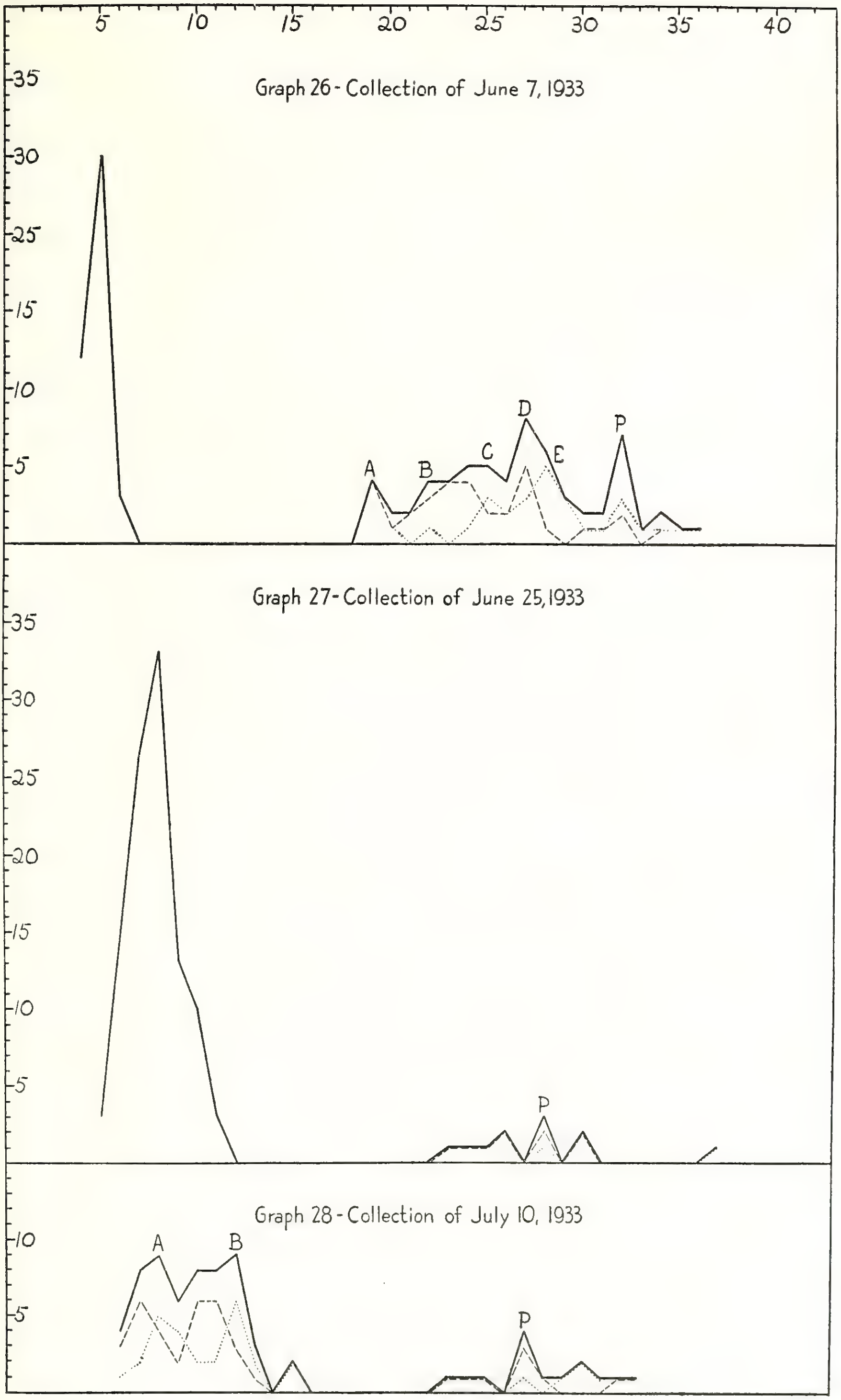
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Graph 26 - Collection of June 7, 1933
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Graph 27 - Collection of June 25, 1933
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Graph 28 - Collection of July 10, 1933
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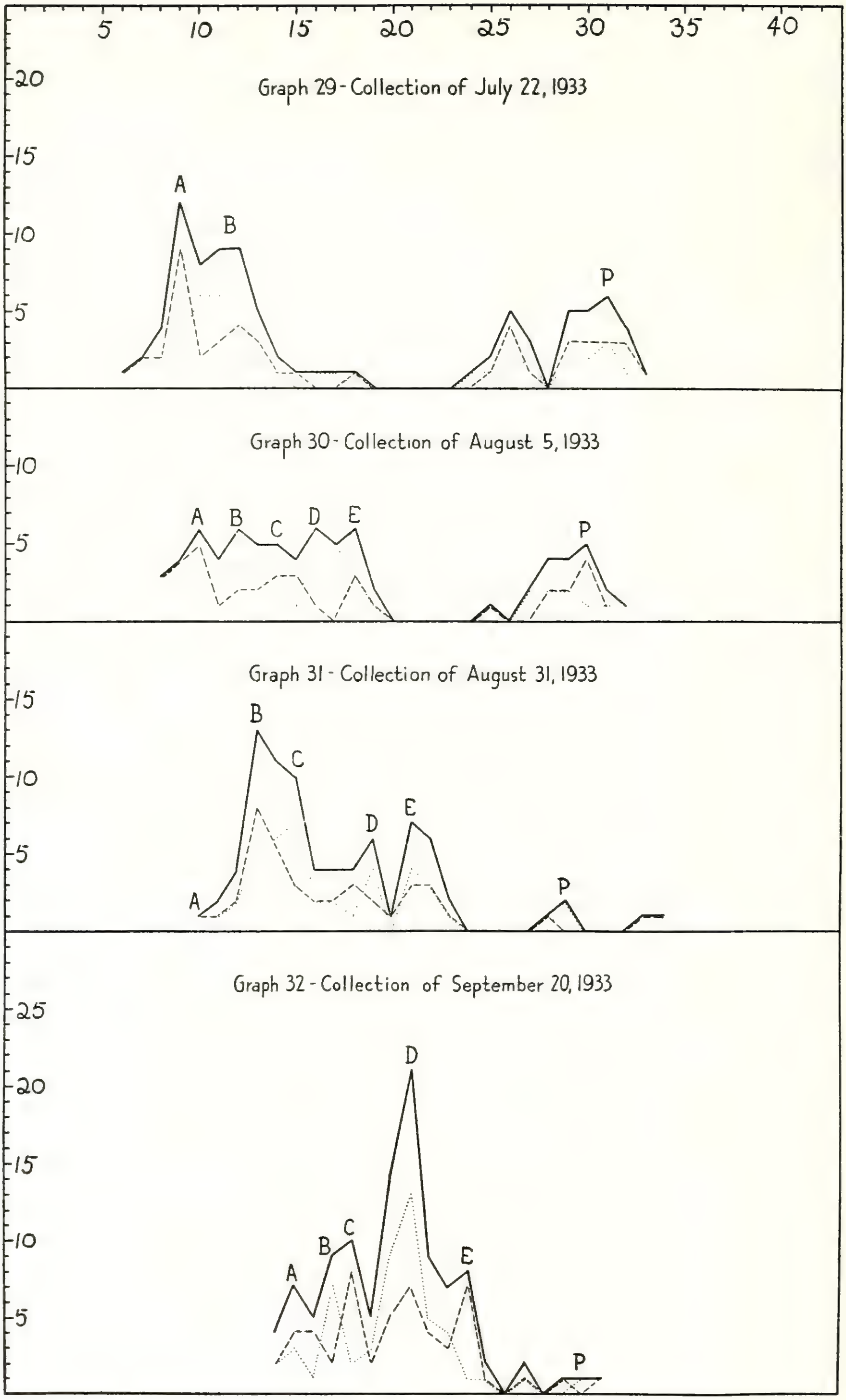

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Graph 29 - Collection of July 22, 1933
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Graph 30 - Collection of August 5, 1933
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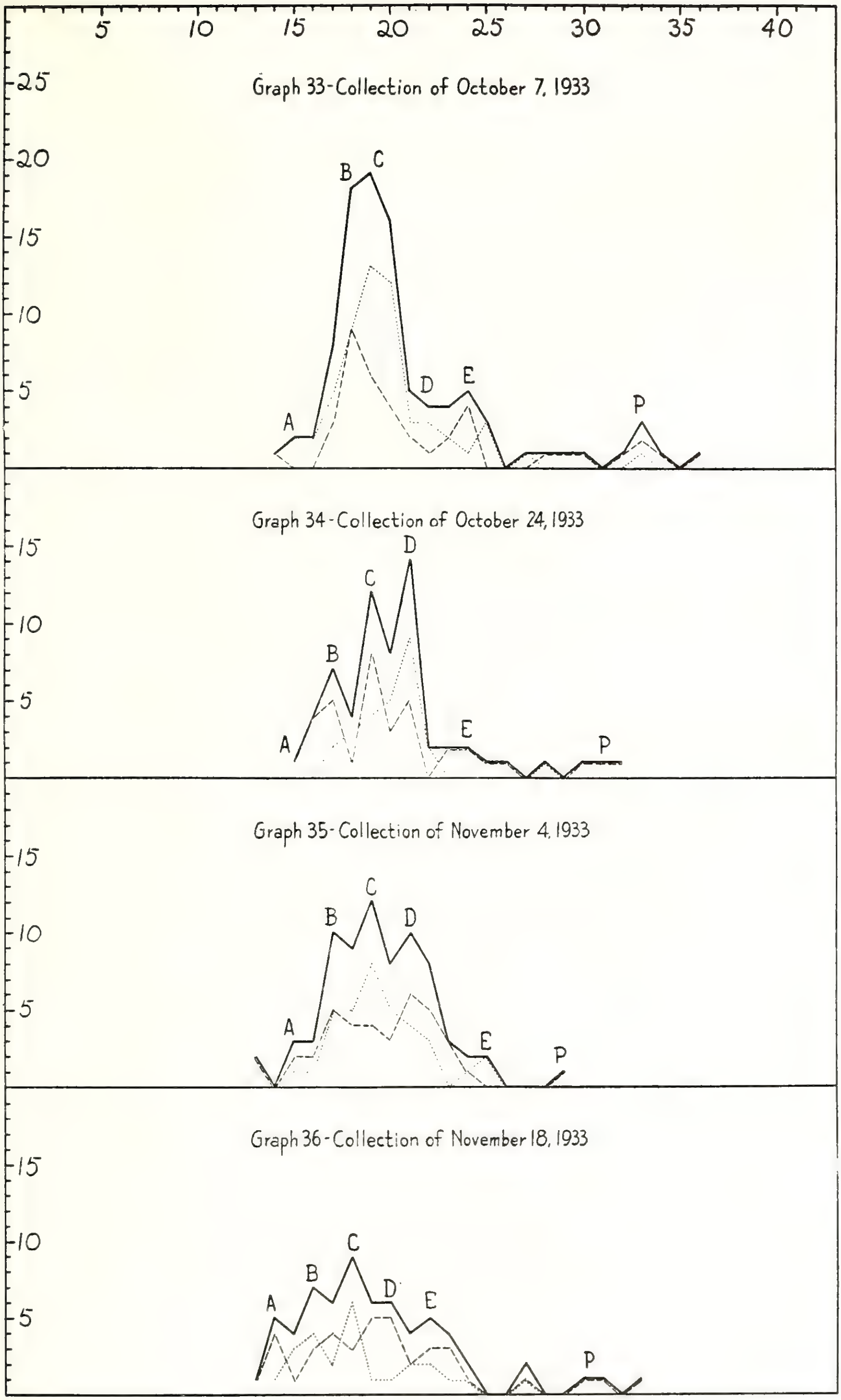
5
A
B
C
D
E
P
Graph 31 - Collection of August 31, 1933
15
10
5
A
B
C
D
E
P
Graph 32 - Collection of September 20, 1933
25
20
15
10
5
A
B
C
D
E
P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15
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25
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35
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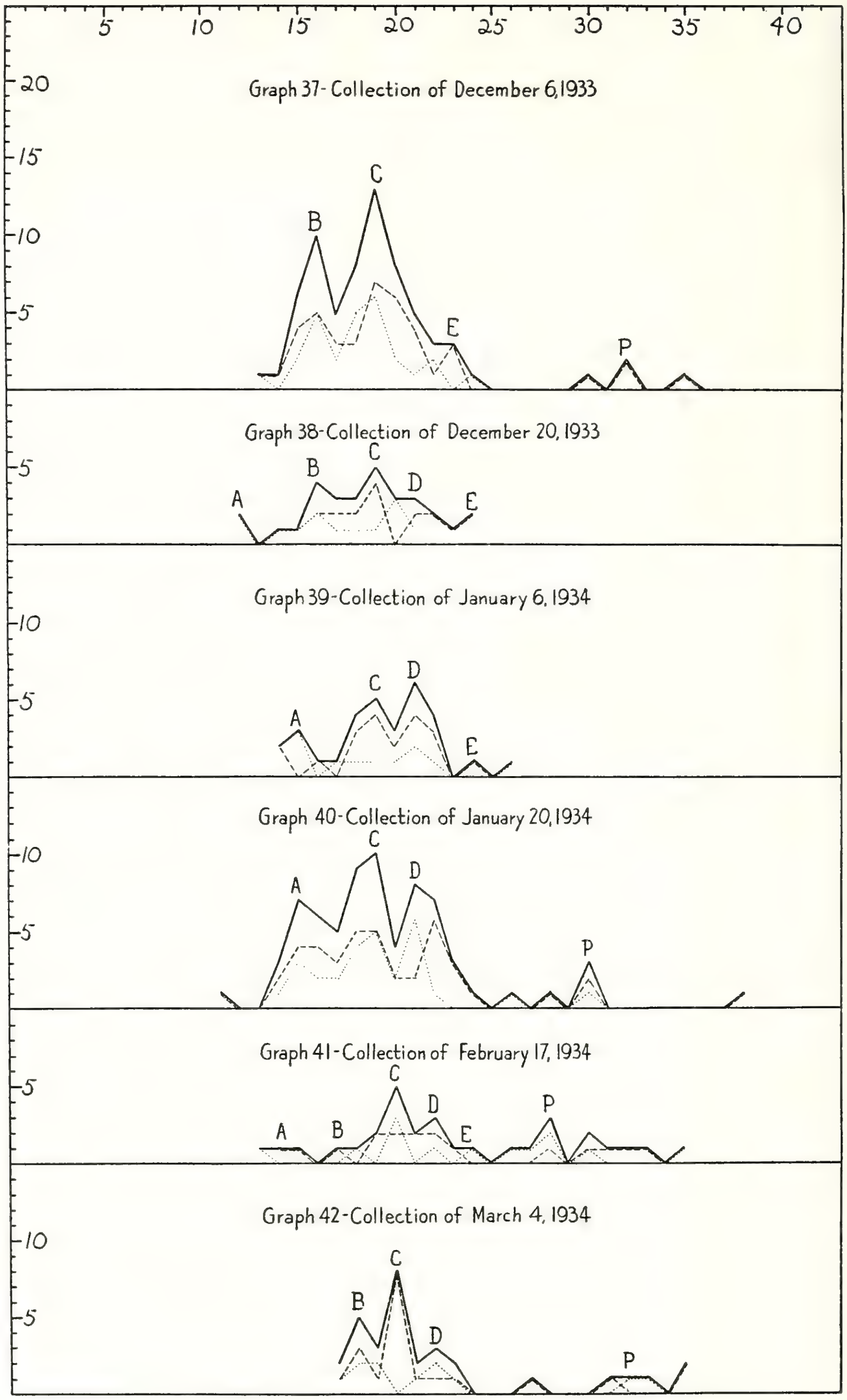
Graph 33-Collection of October 7, 1933
Graph 34-Collection of October 24, 1933
Graph 35-Collection of November 4, 1933
Graph 36-Collection of November 18, 1933
A
B
C
D
E
P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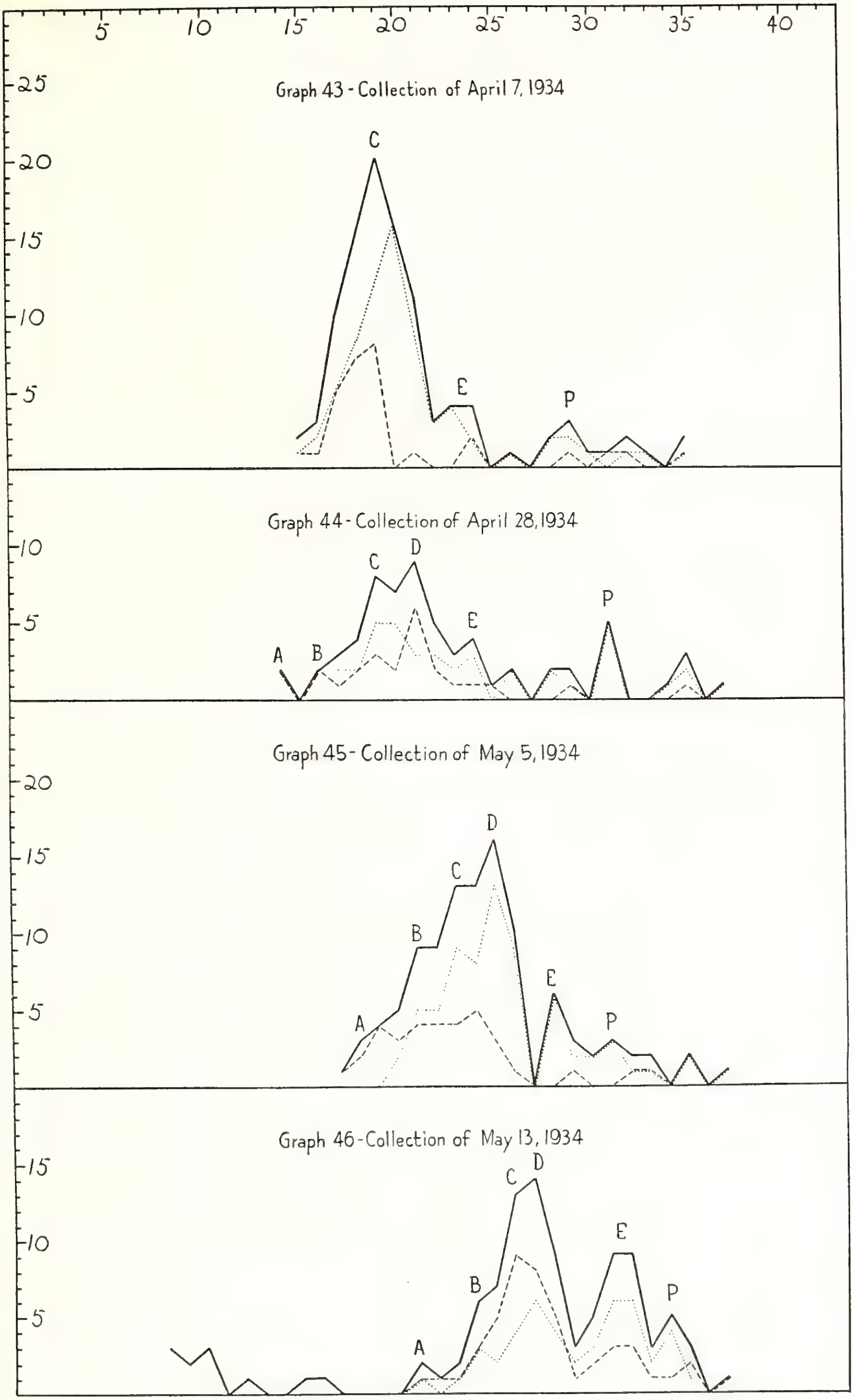
Graph 37- Collection of December 6, 1933
Graph 38- Collection of December 20, 1933
Graph 39- Collection of January 6, 1934
Graph 40- Collection of January 20, 1934
Graph 41- Collection of February 17, 1934
Graph 42- Collection of March 4, 1934



5
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35
40
Graph 43 - Collection of April 7, 1934
C
E
P
25
20
15
10
5
Graph 44 - Collection of April 28, 1934
A
B
C
D
E
P
10
5
Graph 45 - Collection of May 5, 1934
A
B
C
D
E
P
20
15
10
5
Graph 46 - Collection of May 13, 1934
A
B
C
D
E
P
15
10
5